

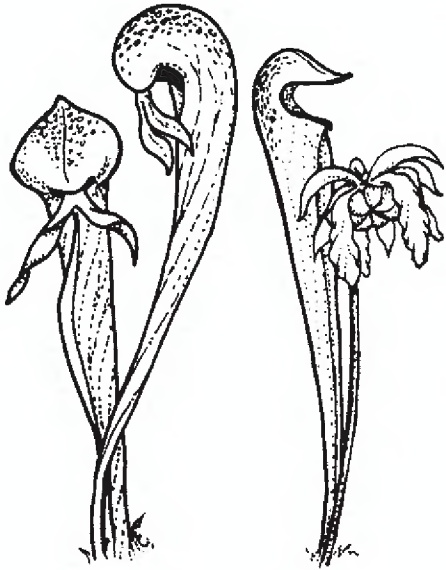
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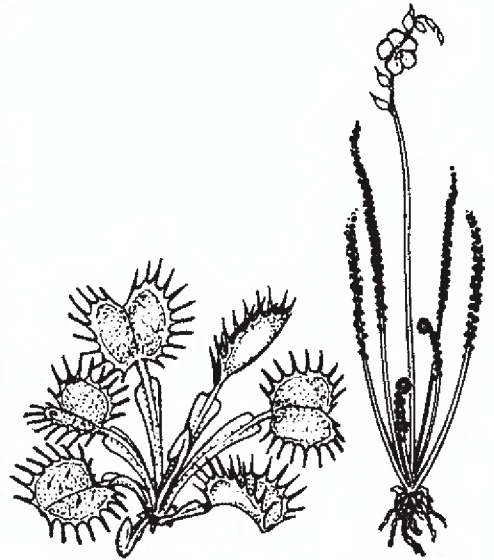




CARNIVOROUS PLANT NEWSLETTER

Journal of the International
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Front Cover: The cultivar *Heliamphora* 'Cyclops'. Photo by Andy Smith. Article on page 141.

Back Cover: The cultivar *Cephalotus* 'OG Black' pitchers. Photo by John Brittnacher. Article on page 103.

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STEVE CLEMESHA (1942 - 2018) – THE LIFE OF A PLANT ENTHUSIAST

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Steve Clemesha (Fig 1) was born in Sydney and developed an interest in botany at an early age. By 9 or 10 he began to grow a collection of native orchids at the family home in North Strathfield. He also began to take an interest in the plants that grew with orchids, both in the wild and in cultivation, and this interest was with him for life.

During his training as a primary school teacher he learnt of North American pitcher plants, which were not grown in Australia at the time. In 1961 Steve received *Sarracenia* seed from Warren Stoutamire. By 1968 Steve's collection included several *Darlingtonia*, a few species and hybrids of *Sarracenia*, and some species of *Drosera*. In 1968 Steve began to correspond with Joe Mazrimas, and through which Steve's collection of carnivorous plants, particularly *Sarracenia*, became far more diverse. Steve was interested in unusual forms of pitcher plants, and he began to make his own hybrids (Clemesha 1991).

In 1976 Steve and his family moved to a five-acre property at Emerald Beach, near Coffs Harbour, where they built their home. Here Steve made several greenhouses, shade houses, and garden beds for his already large and diverse plant collection, that included ferns, bulbs and orchids. The property had a dam, on which Steve grew his *Sarracenia* collection in floating polystyrene boxes (Fig. 2).

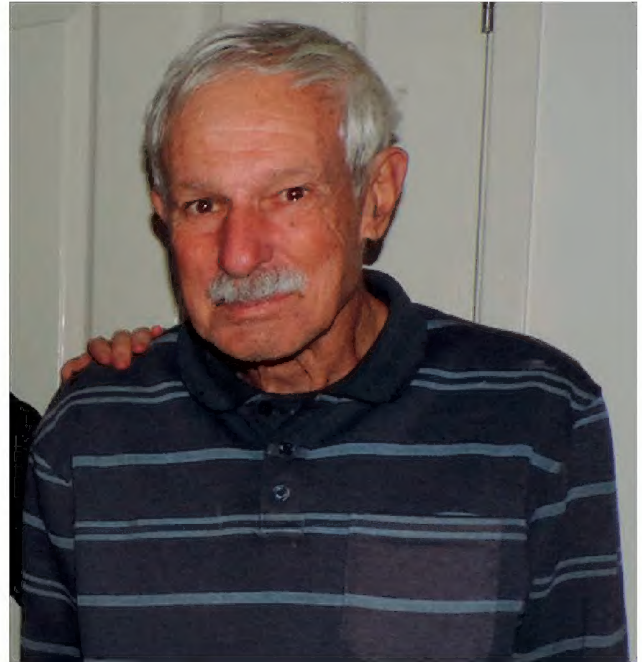


Figure 1: Steve Clemesha on 28 May 2017.

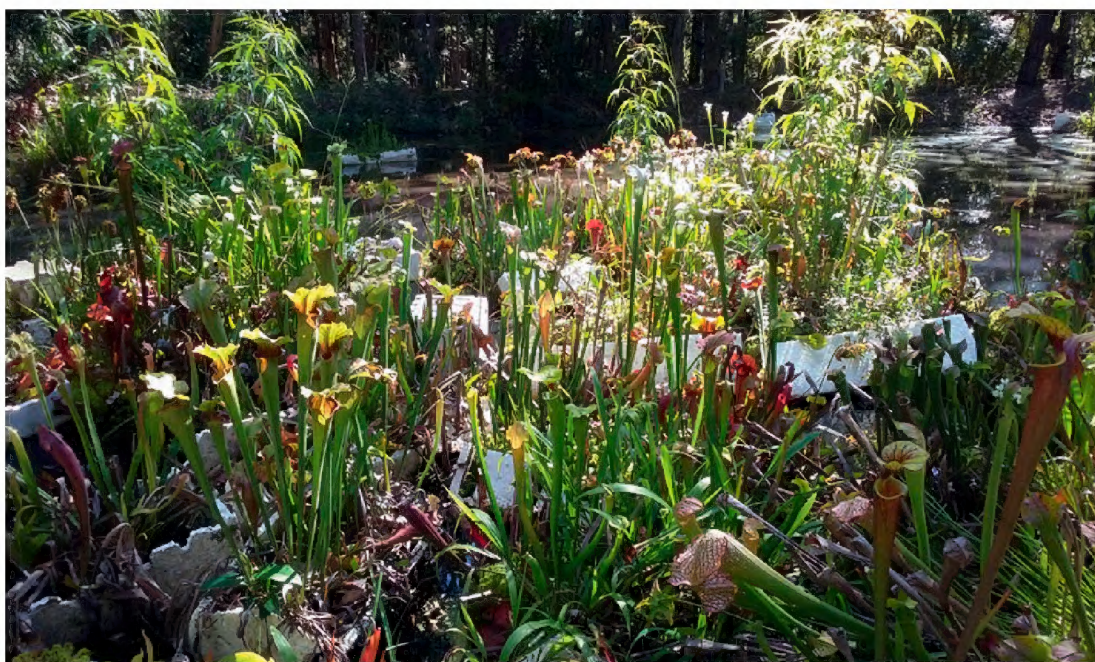


Figure 2: Some of Steve's floating *Sarracenia* collection on 28 May 2017.



Figure 3: A plant of *Drosera anglica* × *filiformis* var. *tracyi* (left); *Sarracenia flava* var. *rubricorpora* × *alata* var. *rubrioperculata* (right).

Steve undertook fieldwork, experimented on growing and propagating plants, created many novel hybrids, wrote numerous articles for the Carnivorous Plant Newsletter, and was a prolific and generous correspondent. Steve was also a passionate conservationist and used his botanical expertise to help argue successfully for the protection of local remnants of native vegetation. Some of his many other achievements include:

- Creating the three-fold informal classification of the *Drosera binata* complex (Clemesha 1972a).
- Preserving *Sarracenia* from populations that have subsequently become extinct.
- Developing the rhizome-notching technique for propagating *Sarracenia* (Slack 1986: pp. 66-67).
- Creating a hybrid between *Drosera anglica* × *filiformis* var. *tracyi* that it is now in collections in different parts of the World (D'Amato 2015) (Fig. 3 left).

Steve's *Sarracenia* hybridization program included at least three different themes: (1) all-red pitcher plants; (2) hairy pitcher plants (particularly using hairy plants of *S. leucophylla* that Steve received from Bruce Pierson); and (3) all-green pitcher plants. Over more than 50 years Steve produced many amazing hybrids, as recognized by Slack (1986: pp. 80-81). Some of the most notable plants include a wonderful form of *S. flava* var. *rubricorpora* × *alata* var. *rubrioperculata* (Fig. 3 right), lurid lime green plants of *S. purpurea* f. *heterophylla* × *rubra* ssp. *jonesii* var. *viridescens*, many different forms of *S. × catesbaei* and *S. × moorei* using different forms of both parental species, and *S. × wrigleyana*.

Sadly, Steve passed away on 17 August 2018. He was 76. He is survived by his wife, Pauline, five children and 13 grandchildren. His plants are grown by many people around the World, and work has commenced on a public display of some of his *Sarracenia* at the North Coast Regional Botanic Garden in Coffs Harbour. His cultivation and propagation techniques have been incorporated into widely accepted best practice, and his ideas for hybridizing *Sarracenia* and the informal names for

the *Drosera binata* complex continue to be used. In short, he has made an on-going legacy. Farewell Steve, you are missed.

Acknowledgements: I thank Steve for his friendship and the knowledge he shared over 30+ years of correspondence. I also thank Pauline for her help and patience as we have been rehousing Steve's *Sarracenia* collection into new homes and establishing a core of collection of his most outstanding plants.

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EVOLUTION OF THE *CEPHALOTUS* PITCHER

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Keywords: *Cephalotus follicularis*, leaf development, evolution, carnivory.

Abstract: *Cephalotus follicularis* (Oxalidales) is a carnivorous plant native to coastal southwest Australia with pitchers that primarily trap ants. The plant also produces non-trapping foliar leaves and occasional intermediate leaves. Close observation of the intermediate leaves plus an understanding of leaf development in angiosperms shows that the pitchers appear to be constructed from five leaflet-equivalent developmental domains that are not separately visible in the pitcher leaf primordia but do map to specific locations. The pitcher development patterns are similar to those of *Oxalis* leaves. Simple developmental shifts can explain the evolution of the pitcher. The pitcher body appears to have evolved from the three leaflets typical of most *Oxalis* species and the lid from two leaflets that arise above the adaxial face of the petiole in a way similar to the adaxial leaflet of *Oxalis tetraphylla*. However, since the lineage consisting only of *Cephalotus* today is 80 million years old, when and how it became carnivorous and developed pitchers remains speculative.

Introduction

Cephalotus is in the monotypic family Cephalotaceae which is part of a basal lineage within the angiosperm order Oxalidales. This order diverged from the other flowering plants approximately 100 million years ago (Li *et al.* 2019). As defined currently, the Oxalidales contain about 1900 species in seven families, including the well-known wood sorrel family Oxalidaceae (Stevens 2017a). Those families most closely related to *Cephalotus*, albeit distantly, include Brunelliaceae, Connaraceae, Cunoniaceae, and Elaeocarpaceae (Cross *et al.* 2019; Stevens 2017a). Based on DNA evidence, *Cephalotus* diverged from its living relatives around 80 million years ago (Heibl & Renner 2012; Li *et al.* 2019). As the various lineages within Oxalidales have all diverged substantially since that time, it is difficult to even guess what their common ancestor looked like. The majority of *Cephalotus*' nearest relatives are large rainforest trees.

Cephalotus has two basic kinds of leaves, pitchers that primarily trap ants but have limited photosynthesis utility (Back Cover) and “foliage” leaves (Fig. 1–2) which provide for photosynthesis especially under low light conditions and during seasons with fewer ants (Nunn 2014; Cross *et al.* 2019). One would think that with 200 years of *Cephalotus* being in cultivation and being studied, there would be a consensus on the developmental biology of *Cephalotus* leaves. There isn't. John Macfarlane's 1889 introduction to his discussion of *Cephalotus* in a paper about carnivorous plant pitchers (Macfarlane 1889) starts out:

The pitchers of this genus [*Cephalotus*] appear to differ in every respect from those just passed under review [*Nepenthes*, *Heliamphora*, *Sarracenia*, *Darlingtonia*], so that no comparison of them can be made. As Dickson clearly showed, the pitcher is a laminar involution, while the lid is a flap of the lamina growing forward over it. Like many other Australian plants therefore it seems to represent one of a chain of forms otherwise lost to us.

Alexander Dickson studied what he considered developmentally teratogenic (abnormal) pitchers (Dickson 1883). At that time *Cephalotus* plants were so precious to the Edinburgh Botanic Garden, he dared not to damage them so all he could do was look. Dickson’s conclusions about how *Cephalotus* pitchers are constructed, with some additions, have remained the dogma to this day:

The conclusions to which I have been led may thus briefly be stated:

- 1st. That the pitcher results from a calceolate pouching of the leaf-blade from the upper surface.
- 2d. That the apex of the leaf is on the far side of the pitcher-orifice from the main axis and from the lid, and is probably represented by the tip of the middle dorsal wing.
- 3d. That the pitcher-lid represents an outgrowth or excrescence from the upper leaf-surface.

The main issues of discussion today relate to “calceolate pouching” and the pitcher lid being an “excrescence”. An example of calceolate pouching is the pouched petal of lady slipper orchid flowers. Calceolate pouching would imply the pitcher is formed by deformation of a leaf element rather than leaf elements merging to form a pitcher. If the pitcher lid of *Cephalotus* is an excrescence, it would mean the lid is essentially an outgrowth of the petiole and not a modified leaflet. Intermediate leaves between pitchers and foliage display pouching as well as hints of other trap elements (Fig. 1). But what do the intermediate leaves tell us about how pitchers and foliage leaves are constructed and how *Cephalotus* pitchers evolved? Are the traps essentially a pouched leaf or is it more complicated?

Materials and Methods

This study was done while propagating *Cephalotus* plants by stem cuttings in the fall. Owing to space constraints, plants were shifted between an indoor terrarium that experienced temperatures of 19°C to 26°C with a 14-hour constant photoperiod and a garage grow area with water trays and humidity domes at temperatures of 10°C to 20°C and a natural and artificial light period based on local sunrise and sunset. Indoors, the range of temperatures were experienced diurnally, while in the garage, temperatures were more constant diurnally but shifted higher or lower every few weeks in accordance to the outdoor temperatures. Under the indoor conditions, mature plants sparsely produce foliage leaves and have not bloomed over a 13-year period. In the garage, the plants produce foliage leaves during the winter and bloom in

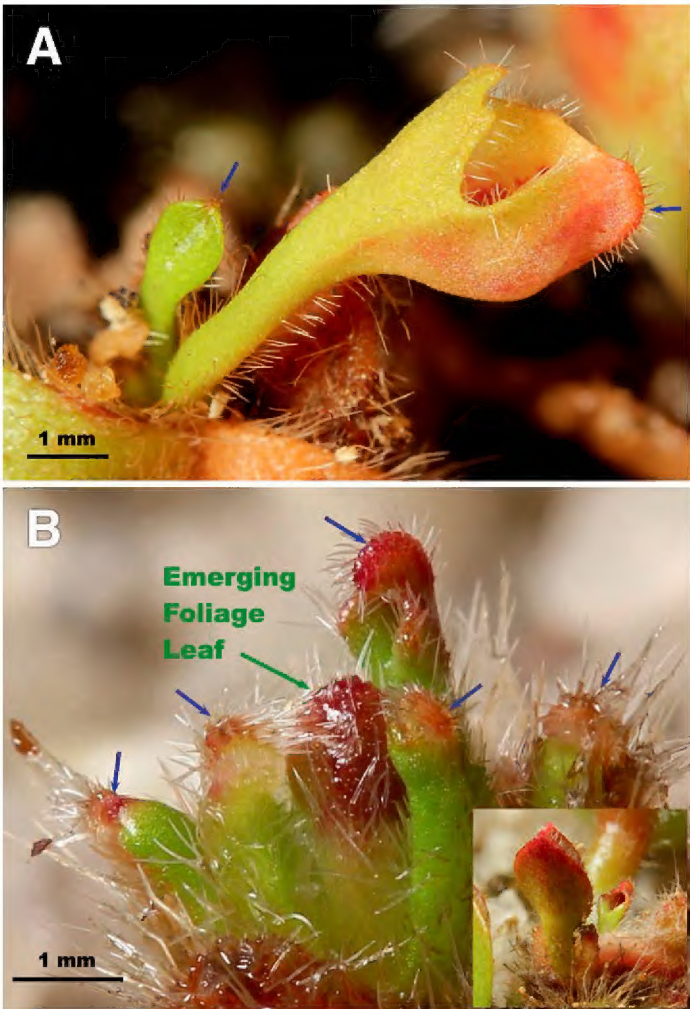


Figure 1: *Cephalotus* intermediate leaves. Blue arrows indicate protrusions that relate to the keel segment on the front of typical pitchers. The **B** inset was taken 40 days after the main image showing mature foliage leaves.

the spring. The *Oxalis tetraphylla* used were standard retail plants purchased locally; sold under the name *Oxalis deppei* 'Iron Cross'. Most of the photos were taken using a Canon DSLR camera and 60 mm macro lens with some photos also using an extension tube. The camera was controlled from a computer by Helicon Remote (www.heliconsoft.com). Multiple images in different focal planes were processed by Helicon Focus to produce what are called focus stacked images. A photo of a 1 mm grid was taken at the same settings and distance and processed with the corresponding set of images to provide a separate image for measurements of scale. Some scale measurements are from direct measurement of the subject.

Angiosperm leaf development

There are essentially two stages in angiosperm leaf development (Champagne *et al.* 2007; Efroni *et al.* 2010). The first stage consists of a leaf primordium arising near a stem apical meristem (see Fig. 2 for an explanation of terms). This would be visible as a very small mound of cells. The stem apical meristem provides the primary axis of orientation for local development using hormone gradients (Fukushima & Hasbe 2014; Yamaguchi *et al.* 2012). The leaf primordium consists of undifferentiated cells also referred to as indeterminate cells. The leaf primordium also sets up a hormone gradient emanating from the far distal side of the primordium (Waites & Hudson 1995). Using these gradients and cell-to-cell communication, the indeterminate cells orient and divide in ways that place cells in a structure that will be used in the second stage. This first stage can have substages if the ultimate leaf is complicated (Bharathan *et al.* 2002). The end result is usually a very small, very vague version of the mature leaf.

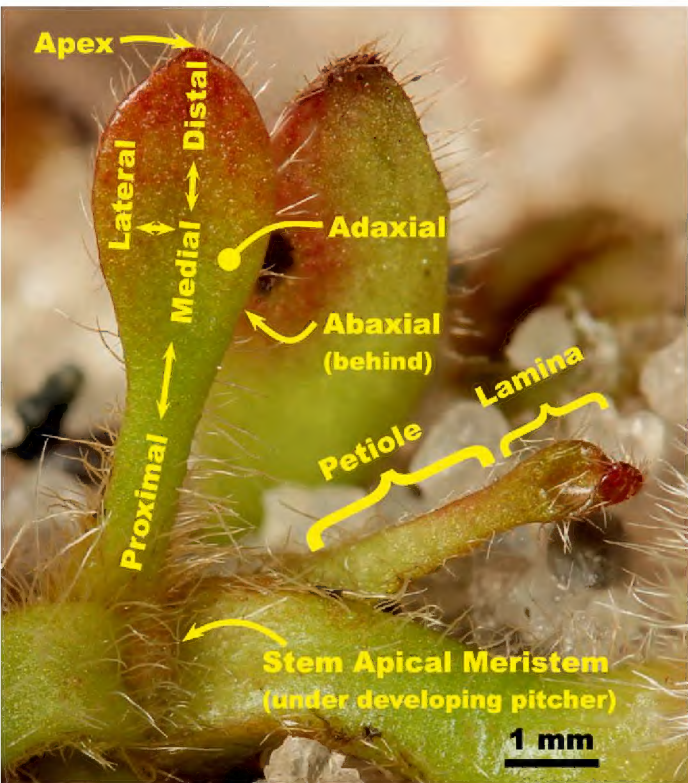


Figure 2: Botanical terms used to describe plant parts. The adaxial face refers to the side of the leaf on the stem apical meristem (SAM) side, abaxial refers to the side facing away from the SAM. Petiole refers to the proximal, stem-like part of a leaf. Lamina refers to the leaf blade or leaflets at the distal end of a leaf.

The leaf development second stage is when the undifferentiated indeterminate cells receive a hormonal signal telling them to differentiate (Efroni *et al.* 2010). The determinate cells may not be fully mature, but their fate is set. The determinate cells communicate among themselves, grow larger and specialize to become the structure of the new leaf. Not all the cells in the developing leaf need to enter stage two at the same time, so again, things can get complicated to make complicated leaves. How plant cells communicate to produce their structures is an emerging field so I will generally use “signaling” here to indicate any sort of communications that could involve hormones like auxin or other chemicals such as small RNAs.

Peltate leaves

Oxalis species such as *Oxalis tetraphylla* (Fig. 3) and *Tropaeolum majus* (nasturtium) provide good examples to help understand *Cephalotus* pitcher development. Not all *Oxalis* species show the characteristics described here. There are important parallels between *O. tetraphylla*

and *Cephalotus* leaf development. The most obvious parallels are both genera have peltate petiole attachment to the leaf lamina and *O. tetraphylla* leaves and *Cephalotus* pitchers develop with leaf tips pointed back at the base of the leaf.

Hagemann and Gleissberg (1996) have superb images showing leaves at the leaf primordium stage including the peltate leaf of *Tropaeolum majus*. Nasturtium is the poster child of peltate leaves and the authors show how peltation occurs in that species. The leaf primordium starts out with the distal side palmate and containing five joined leaflet primordia looking like a maple leaf. As the petiole grows and becomes round, two more leaflet primordia appear on the proximal side producing a lopsided, seven-point crown. Hagemann and Gleissberg describe the appearance of the new leaflet primordia as growth from around the leaf primordium forming a new ridge on the proximal side for the new primordia. Fukushima and Hasbe (2014) refer

to this ridge as the “cross zone”. The cross zone effectively crosses the proximal, inner/adaxial part of the future petiole. It is what changes a sided palmate leaf to a peltate leaf.

It is unfortunate the use of the words “adaxial” and “abaxial” can make the discussion of leaf development confusing. I will be redundant to help make the discussion clear. Adaxial and abaxial can be used to indicate direction or orientation as in the adaxial/abaxial development axis. The words can also specify the faces of leaf elements corresponding to that axis. The adaxial face of a leaf element is usually the inner side facing the apical meristem or the upper sun-facing side. The abaxial face is the outer side facing away from the apical meristem or the lower shaded side. In most leaf types, the assignment of adaxial or abaxial is quite straightforward. In peltate and pitcher-like leaves, assignment of leaf faces can be difficult because it may not be clear how to assign leaf structures that arise from the cells in the cross zone. In describing leaf development, it is critical to be able to keep track of structural orientation.

Adaxial/abaxial confusion can be seen in *O. tetraphylla*. *O. tetraphylla*, as the name implies, has four leaflets while most *Oxalis* species have three leaflets. The fourth leaflet is above the inner/adaxial side of the petiole. The adaxial part of the petiole of *O. tetraphylla* can be traced explicitly because it starts out flat and shifts to rounded (Fig. 4A-C). Where the flat petiole margins disappear, the petiole becomes a rounded “D”-shape with the flattened part being the inner/adaxial face. This flattened area can be traced all the way to the leaflets in *O. tetraphylla* leaves with three leaflets as in Figure 4A. In the typical four leaflet leaves, the petiole is rounder and it is difficult to trace the flat area the last few cm to the leaflets. The critical observation is that at no point along the petiole do the margins of the flat area come together as would be expected if the inner/adaxial face associated with this flat area was pinched off. The petiole just becomes round. In *Cephalotus* the petiole is definitely “D”-shaped (Fig. 4D-E) until right before it attaches to the pitcher. The veins in the proximal flattened part of the *Oxalis* leaf form an arc as is typical in non-peltate leaves (Fig. 4C). In both species, the petiole veins are in a circle in the rounded part (Fig. 4B,D-E).



Figure 3: *Oxalis tetraphylla* plants. Notice the strong midrib on each leaflet. The leaflets only open in bright light. Under dim light and darkness, the leaflets fold at the midrib and point down by hinging at the leaflet base.

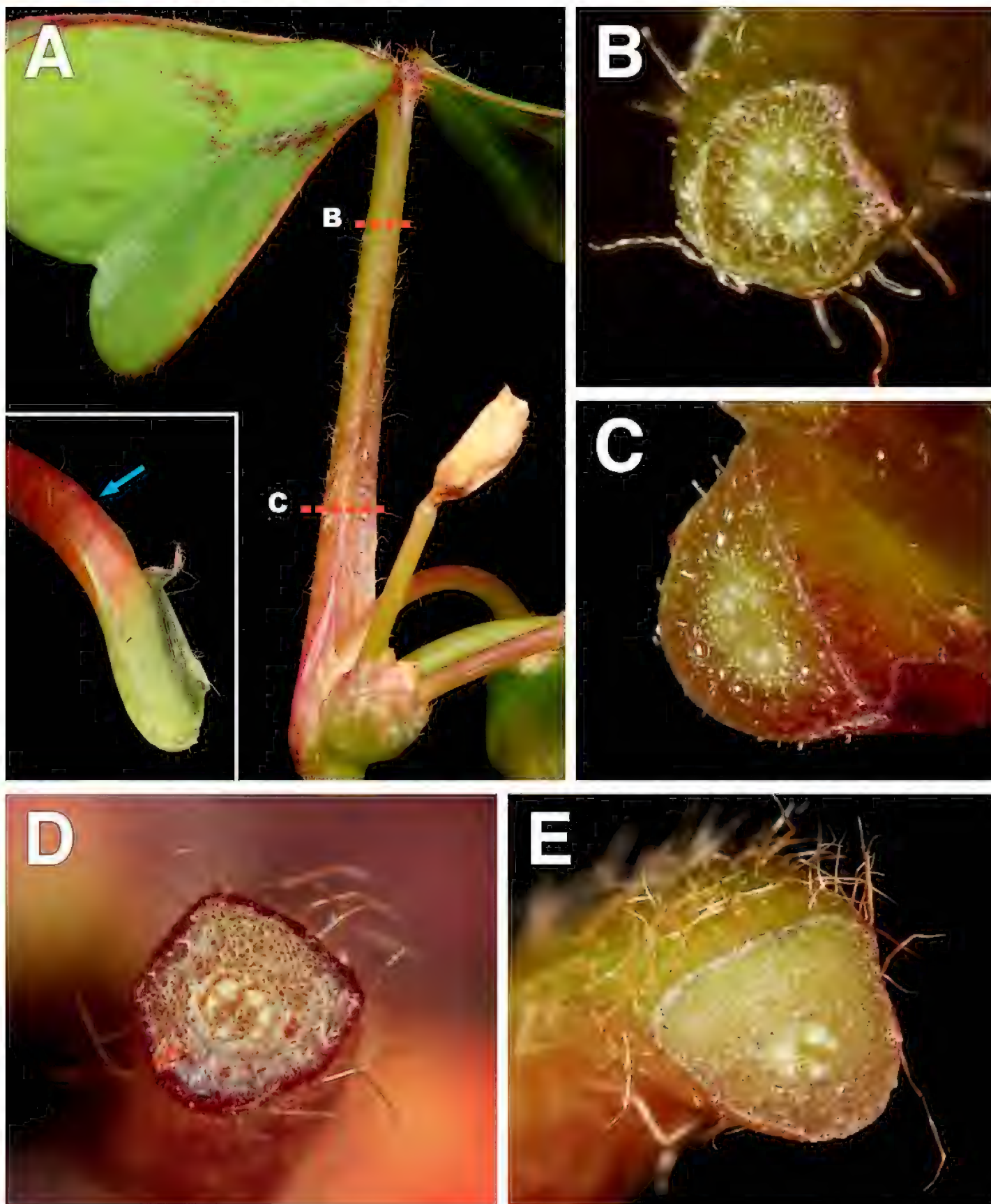


Figure 4: The main image in **A** is a three-leaflet leaf of *Oxalis tetraphylla* from the top of a flower scape. The orange dotted lines are where cross sections were taken for images **B-C**. The inset in **A** is a four-leaflet leaf petiole from a flower scape. The blue arrow in the inset is where the leaf margins fade. **D-E** show cross sections of *Cephalotus* pitcher petioles.

Leaf margin signaling is not well understood (Fukushima & Hasbe 2014), but I believe the circle of leaf veins occurs because of the lack of leaf-margin signaling rather than a loss of adaxial/abaxial signaling. This is because in peltate leaves, the leaf components maintain an adaxial/abaxial orientation throughout development. This is important because it means there is no special set of

developmental rules for peltate leaves. Peltation simply results from one end of a continuous range of variation in the balance of adaxial/abaxial signaling and leaf-margin signaling. In peltate petioles the adaxial/abaxial balance is somewhat shifted adaxially and the leaf-margin signaling is suppressed. If leaf-margin signaling was not disabled in peltate leaves where the petiole terminates at the base of the leaf lamina, the leaf lamina would open up and thus not be peltate.

Oxalis leaf development

The shape of the leaf primordium reflects the ultimate structure of the leaf. Typical *Oxalis* leaves have three leaflets. Based on other genera with peltate leaves where there are published images, the leaf primordia of an *Oxalis* with three leaflets should look like a crown with three points. *O. tetraphylla*, with its four leaflets, should look like a crown with four equally spaced points. The fourth point or leaflet primordia would be on the inner/adaxial side of leaf primordia proximal to the stem apical meristem in the cross zone.

As the leaf of *O. tetraphylla* develops, all of the leaflets develop at the same time (see Fig. S3 in Bharathan *et al.* 2002 or Champagne *et al.* 2007 for images of a different *Oxalis* species), but the petiole grows asymmetrically to produce an almost 180° bend in the inner/adaxial direction pointing the leaflet tips toward the apical meristem (Fig. 5). At this stage in *O. tetraphylla*, the major

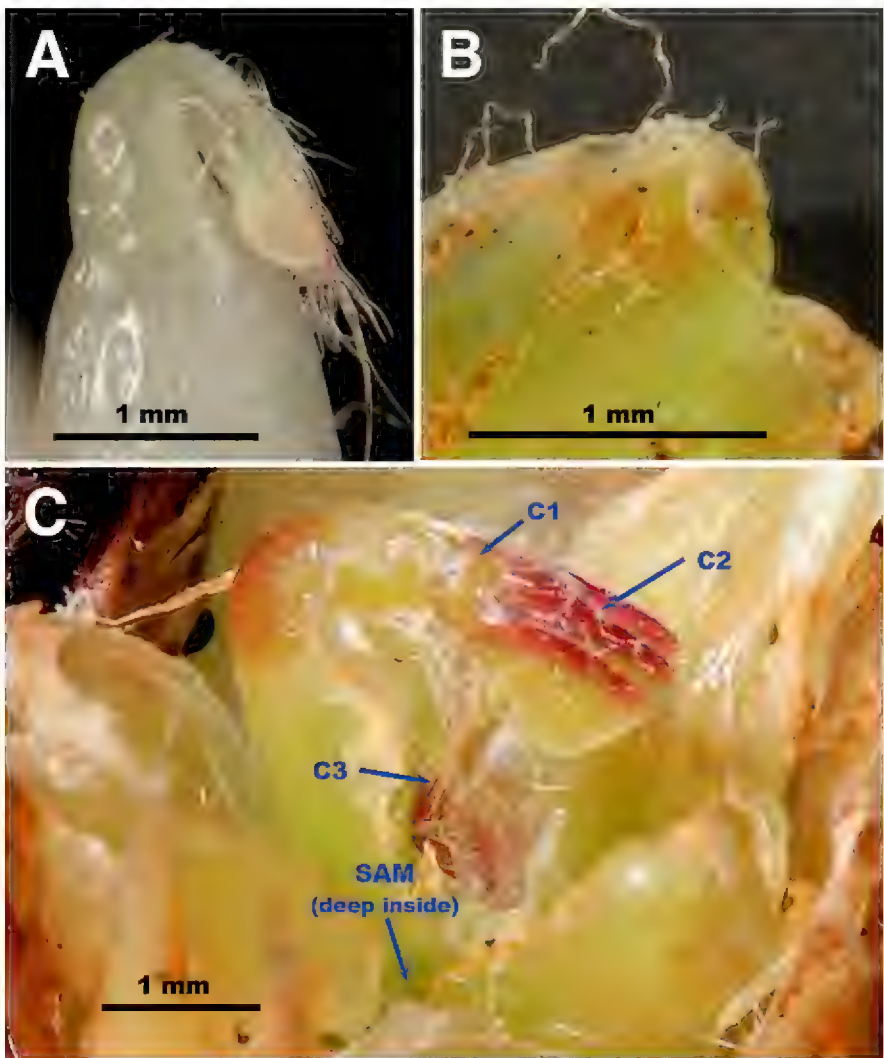


Figure 5: Developing leaves of *Oxalis tetraphylla*. **A** shows the first leaf produced by a bulbil. **B** is a developing leaf dissected from a bulb. **C** shows two leaves excavated from a bulb. **C1** will become the hinging leaflet base; **C2** are the leaflets; **C3** is a second leaf.

leaflet vein of all three outer/abaxial leaflets face away from the arched petiole and the leaflet leaf segments are folded toward the petiole. The fourth leaflet is attached to the inner/adaxial region of the petiole proximal to the arch of the petiole. The major leaflet vein is on the side under the petiole arch with the leaflet segments folded away from the petiole among the outer/abaxial leaflets. When *Oxalis* species with bulbs are buried, having the petiole bend and leaflet tips pointed toward the apical meristem allows each leaf to push up through the same hole to the soil surface. This helps keep the leaflets from being damaged during their journey to the surface. When the leaves reach their ultimate height, the cells on the inner/adaxial side of the petiole grow to orient the sun side of the leaflets upward.

Cephalotus pitcher development

In plants, one cannot generally use “ontogeny recapitulates phylogeny” to help understand the evolution of a species. All angiosperms go through the same basic developmental steps and there are no bizarre relics of past designs like we find in animals. In plants, that means studying relatives instead. However, the comparison to *Oxalis* does not hold for the initial leaf primordium. In fact, the leaf primordium of *Cephalotus* looks more like the one for *Sarracenia purpurea* (Fukushima *et al.* 2015), except in *Sarracenia* the leaf primordium wraps the apical meristem rather than being off to the side as in *Oxalis* and *Cephalotus*. Figure 6A is a drawing based on a scanning electron microscope image from Froebe and Baur (1988) where I have indicated where cells are staged for later development. This arrangement is drastically different from “normal” flat leaves.

In *Cephalotus*, the equivalent of the *Oxalis* leaflet most distal from the apical meristem develops first. This developmental domain arches over the top of the primordium in *Cephalotus* but does not in *Oxalis*. It is typical for the primordium to go from indeterminate to determinate in a wave from the top/distal point down (Yamaguchi *et al.* 2012). That is what happens here. What is first seen in

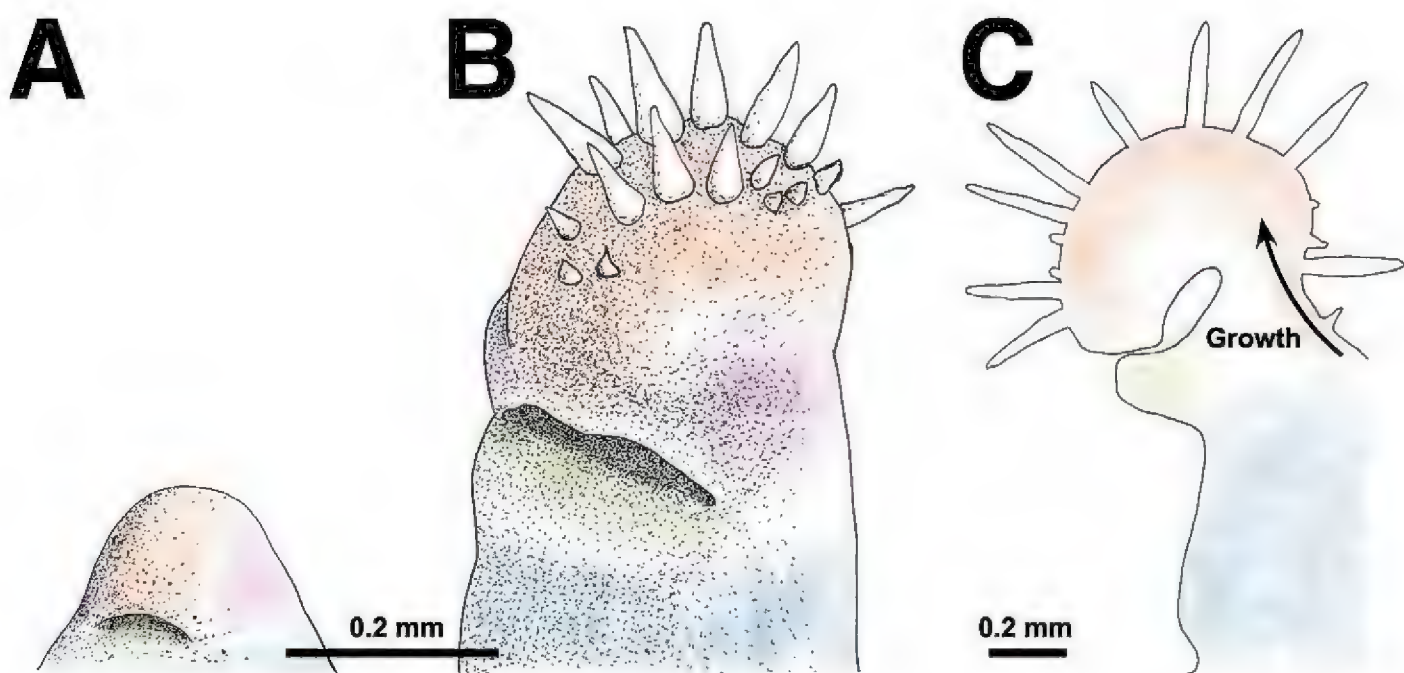


Figure 6: Drawings showing the growth of *Cephalotus* pitcher primordia with different shading colors representing approximate locations of development segments. The drawings **A-B** are based on scanning electron microscope images and **C** on a light microscope longitudinal section image in Froebe and Baur (1988). Orange shading corresponds to the front keel developmental domain, violet to the side wings, green to the lid, and blue to the petiole.

the developing primordium is the ridging and hairs of the front keel of the pitcher (Fig. 6B which is based on Froebe and Baur 1988 Figs. 9–12). The lateral wing leaflet domains expand as necessary to accommodate the growth of the front keel but do not appear to differentiate. Nothing much happens to the proximal leaflet domains destined to be the lid at this stage. As the keel grows, it opens up the inside of the leaf, forming a pitcher (Fig. 6C based on Froebe and Baur 1988 Fig. 15).

The pitcher continues to develop in a looping manner similar to *O. tetraphylla* leaves with *Cephalotus* having an approximately 90-degree bend near the distal end of the petiole. Typically, when the developing pitcher is about 1 mm long, the petiole is very short and the pitcher covers the apical meristem with the keel pointing up (Fig. 2). At a pitcher length of 2 mm the petiole is longer and the lateral wings have formed as well as the lid, but the back of the pitcher has not formed (Fig. 7A). Note how the keel, lateral wings and lid radiate directly from the petiole attachment in a way reminiscent of *Oxalis*. When the pitcher back finally grows, it straightens the curved front keel with

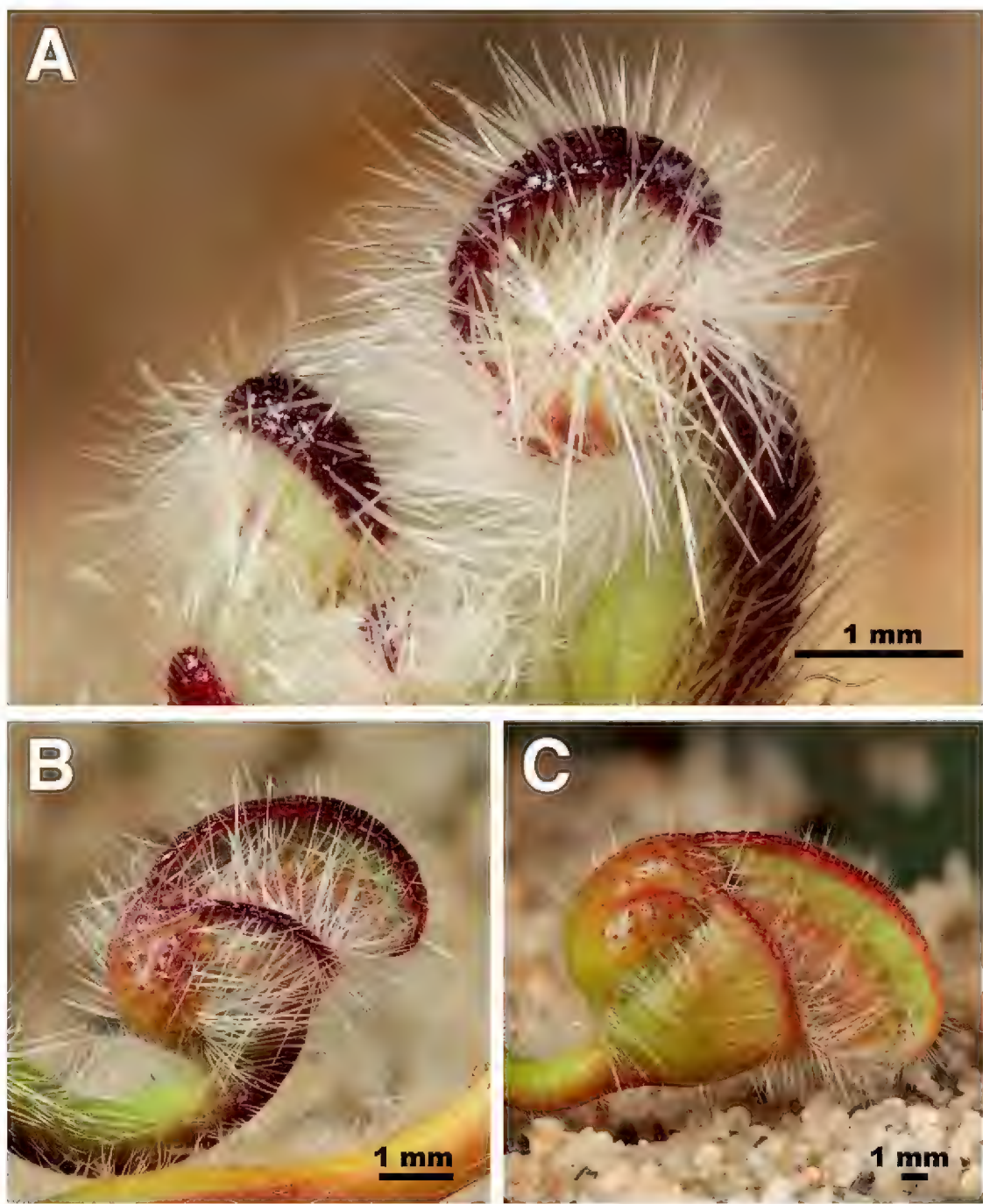


Figure 7: Developing *Cephalotus* pitcher. Notice in **A** the petiole makes a 90° bend and how the bases of the keel, side wings, and lid come together at the petiole. In **B-C** the elements are separated as the pitcher back expands.



Figure 8: *Cephalotus* seedling. The first true leaf is a foliage leaf. The juvenile pitchers lack some of the intricacies of adult pitchers.

the result that the final form of the pitcher is determined. It is in a position essentially laying on its back with the apex of the keel pointing back at the apical meristem (Fig. 7C). The petiole continues to grow to push the pitcher away from the stem apical meristem. In compact plants with many pitchers, the bottom of the pitcher acts as a battering ram to get the new pitcher past older pitchers and into the light. When the pitcher is in place, the cells on the inner/adaxial side of the petiole where it attaches to the pitcher grow to flip the pitcher upright and finish the expansion of the back. The juvenile and adult pitchers display all these features although the juvenile pitchers are somewhat simplified (Fig. 8), likely owing to different prey species.

Cephalotus foliar and intermediate leaves

Based on morphological studies, *Cephalotus* foliar leaves are expanded petioles (Arber 1941; Lloyd 1942; Franck 1976) although these and other authors may not put it so bluntly or they use the word “petiolate”. DeGreef (1990) suggested the foliage leaves are “inhomogeneous, teratological structures” because the base, or “petiole”, of the foliar leaves show typical peltate circular arrangement of veins which then flare out in the upper widened flat “lamina” part of the leaf. If circular arrangement of the veins results from a loss of leaf margin signaling, then all it would take is the leaf margin signaling to be turned on to widen the leaf and flare out the veins. Otherwise

there is little remarkable about the foliage leaves other than they are quite simple and both faces are similar. *Eucalyptus* is a good example of a bifacial leaf where both faces can be essentially the same in order to allow maximal photosynthesis from light penetrating both sides (Evans & Vogelmann 2006).

Cephalotus has a complete range of intermediate leaves that can appear in the fall and winter. The types of intermediate leaves include foliar leaves that are dished or pouched with just a hint of the keel on the outer/abaxial side or foliar leaves with one knobby spot of red at the apex containing a tuft of long hairs, to leaves that appear to be almost functional incompletely differentiated pitchers. Figure 9A-B show a dished foliar leaf with a small pitcher keel on the outer/abaxial side. It appears the presence of the keel induces the leaf to dish. Figure 9C-E show the development over time of a sided palmate intermediate pitcher after the petiole has grown to its ultimate length. Initially there are four hair tufts and a small front keel. Notice how the keel initially covers the center top of the petiole and later bends up. This leaf has some leaf-margin signaling which opens up the space between the two tufts corresponding to what could have been a lid. As the leaf matures, the keel and lid components become more prominent although the lid components show no hint of producing a lid at maturity. The five leaflet components can be seen clearly in the mature leaves in Figure 10A-B. Figure 10D-F show pitcher-like leaves with an entire lid. They have different degrees of “back” development, which in these intermediate pitchers is the bottom. Figures 11–12 show more intermediate leaves with various developmental patterns. Figure 12A is most interesting because it is a sided palmate intermediate leaf where the domains I have identified as “lid” form clear patches like typical pitcher lids.

In the intermediate leaves seen in this study, the front keel is the developmentally dominant segment and it does tend to bend the way that segment does in typical pitchers, but the petiole does not bend to project the keel forward. Instead the keel projects down. In the intermediate leaves with definite lids, the lid projects distally rather than adaxially toward the flat side of the petiole (Figs. 1A, 10D-F, 11E-F). Again, this is because the petiole does not bend as seen in Figure 7A. Intermediate pitchers are built straight up and out instead of on their backs and then flipped up. It appears that for each intermediate leaf, the petiole and lamina are each running a different mix of pitcher and foliar leaf development programs. The palmate intermediate leaves have more leaf margin signaling with the lamina tending toward a foliar leaf. The simplified pitchers lack the definite leaf margin signaling that would pull the pitchers apart but also lack the complex developmental patterns to produce a typical pitcher that would work to catch ants.

Cephalotus can also produce miniature flower scapes. Figure 9F shows a 4.5 mm long petiole with a 5 mm long flower scape containing what appear to be tiny flower buds at the apex. Cross *et al.* (2019) surmise that intermediate leaves, which also apply to this case of miniature scapes, occur as a result of stress during changing seasons. Flower scapes appear in the early spring. *Cephalotus* likely has a temperature-dependent development control which could be used to study general questions in plant developmental biology in a similar way as a temperature sensitive mutant in *Antirrhinum majus* (snapdragon) that was used by Waites and Hudson (1995). To do such studies would require a determination of the parameters that trigger intermediate leaves.

What is most important about intermediate leaves from an evolutionary standpoint is we can identify how leaf construction is compartmentalized in a leaf where we cannot actually see individual leaflet primordia. We see five developmental domains in intermediate leaves. Each domain is likely equivalent to an ancestral leaflet. We cannot see leaflet primordia in the images of Froebe and Baur (1988) because they studied normal pitcher primordia which have the leaflet primordia fused. The primordia of intermediate leaves probably have interesting details.

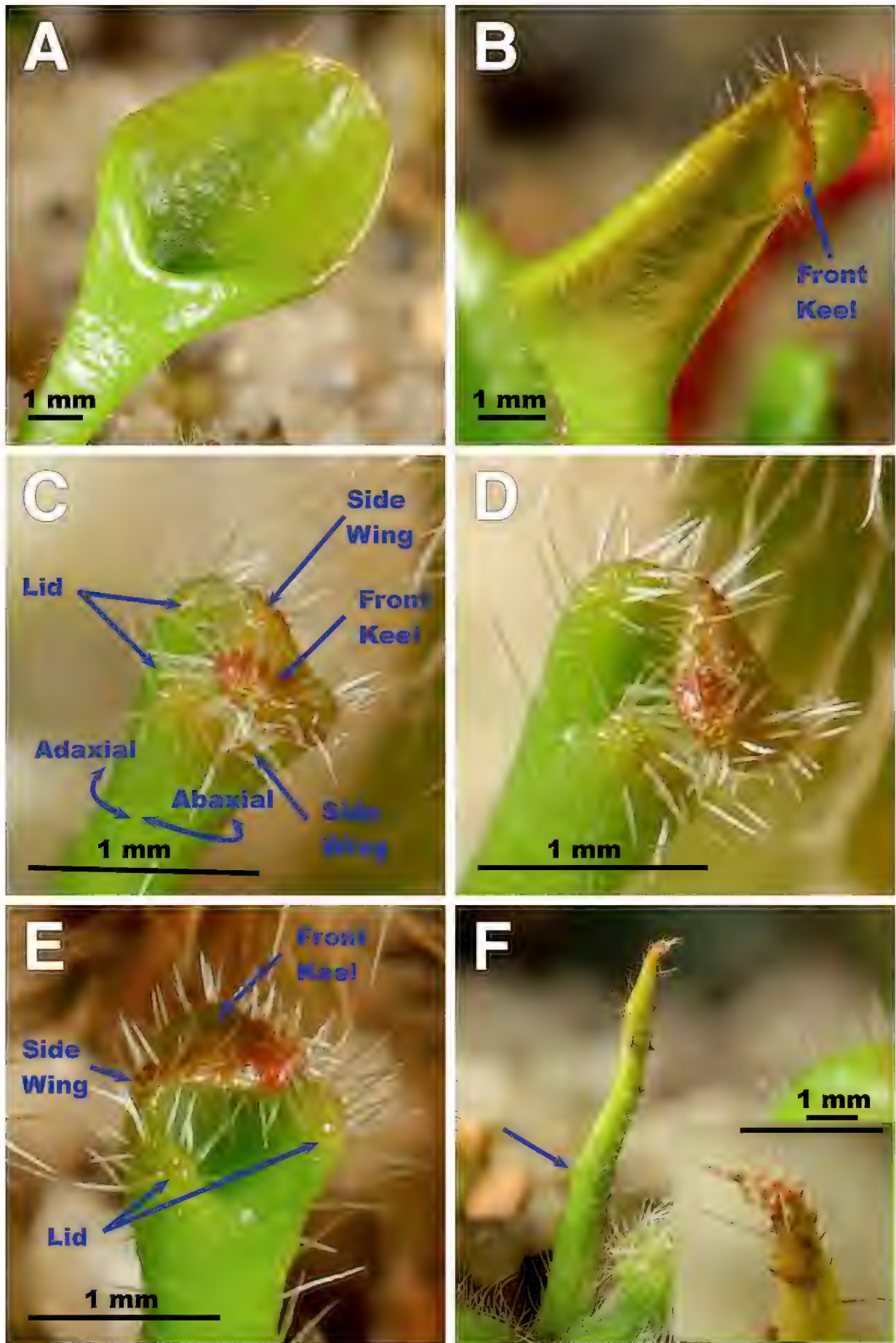


Figure 9: **A-B** show a pouched foliar leaf with a keel on the abaxial side (arrow). **C-E** show a developing intermediate leaf. Of the five leaflet primordia, only the keel makes a recognizable feature. The leaf developed a small dead area which resulted in the keel skewing to the side as it matured. **F** is a needle-shaped leaf that appears to be a miniature flower scape. From the apical meristem to the arrow, the scape is “D” shaped in cross section like a petiole. At the arrow it transitions to nearly round. The apex appears to have tiny flower buds.

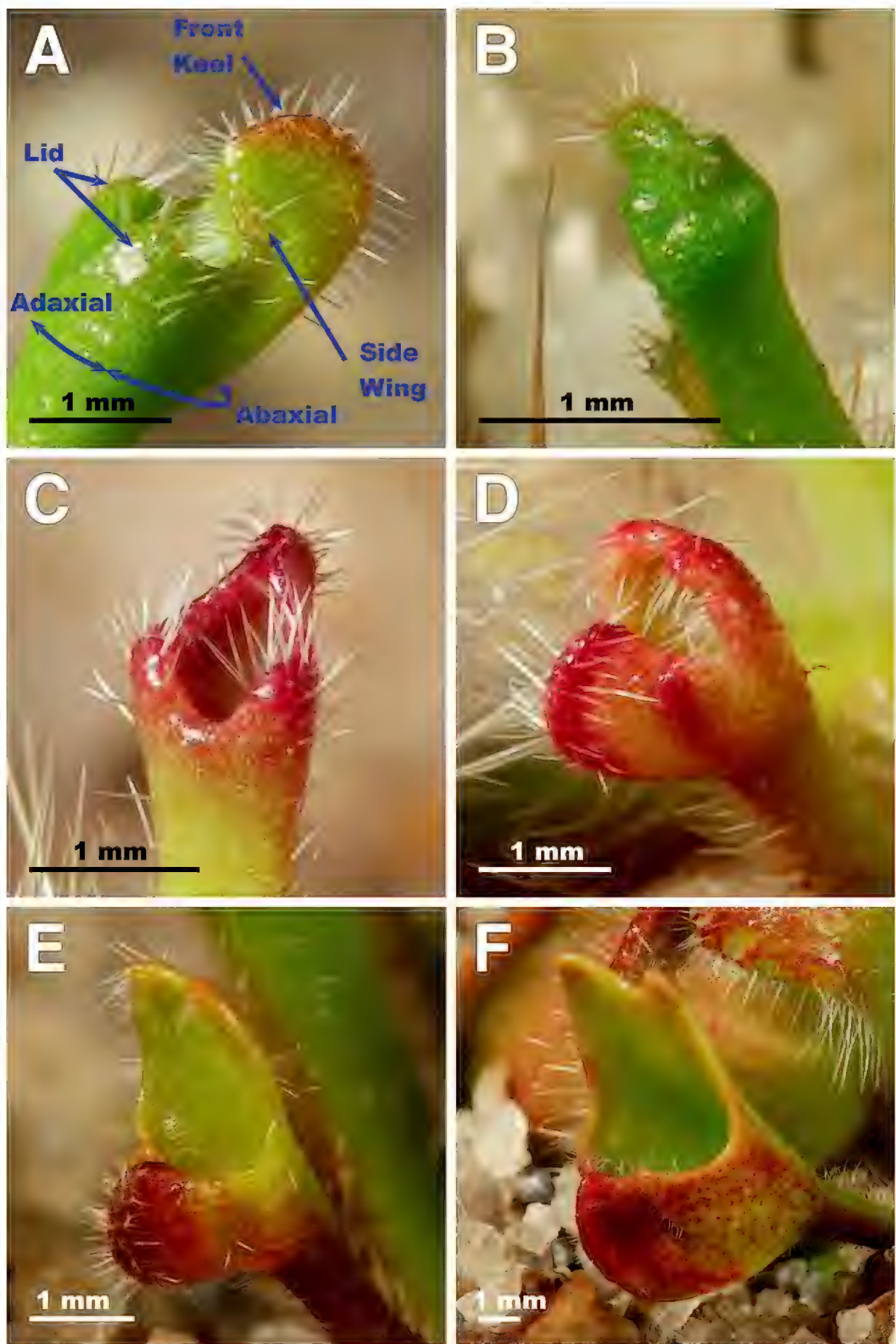


Figure 10: Mature *Cephalotus* intermediate leaves. **A-B** show the leaflet developmental domains. **B** did not develop beyond the point shown. **C** is a sided palmate intermediate leaf. **D-F** are peltate intermediate pitcher leaves. **D** has all the developmental domains terminating at the petiole. **E-F** have an expansion along the bottom that is similar to what is seen in typical pitcher backs.

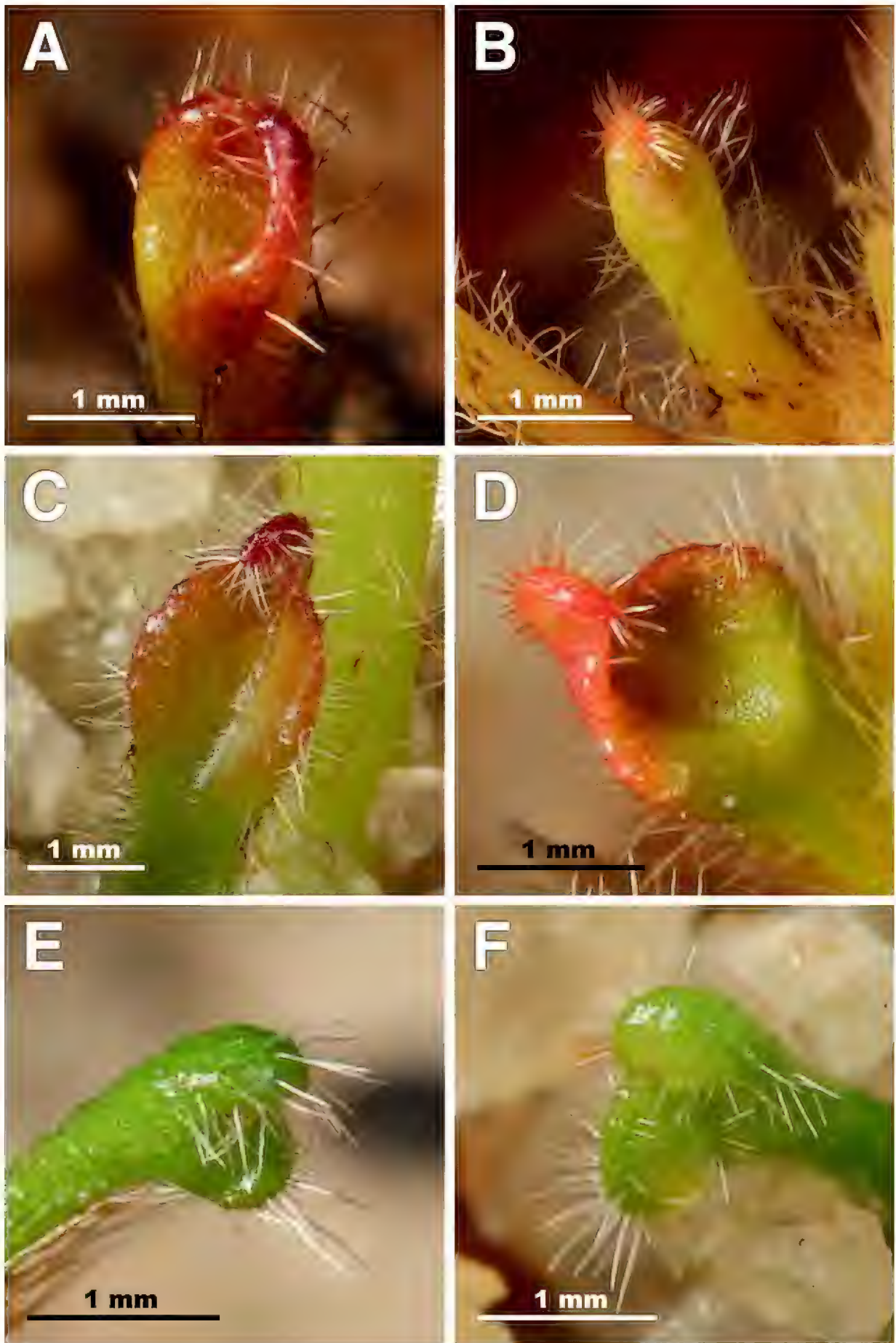


Figure 11: Additional examples of *Cephalotus* intermediate pitchers. **A-D** show various degrees of foliar leaf influence. **E-F** show how without the 90° adaxial bend in the petiole, the pitcher-like intermediate leaves develop in an upright position with the keel arching down.



Figure 12: In this this study, I did not observe any palmate intermediate leaves showing characteristics of a lid in the inner/adaxial developmental domains I refer to as “lids”. Robert Gibson kindly provided image **A** that shows clear areas as seen in typical *Cephalotus* pitchers. Note the unusual intermediate leaf in the background as well. Gibson also provided the image **B** showing a large intermediate pitcher. Clayton (2013) also observed large intermediate pitchers. Note in this case the side wings are missing or displaced to the bottom of the pitcher. The mouth teeth are present but obscured by nectar. The usual trace of hairs that separate the side wing domain from the lid domain is present.

Cephalotus leaf evolution

It is easy to say that the pitchers of *Cephalotus follicularis* evolved from a compound leaf. But it is not so easy to understand exactly how that happened. How does a plant lineage reliant on photosynthesis in compound leaves evolve to be dependent on nutrients from captured prey in pitchers? Every single step the plants take in that process must make sense for their current situation. The plants that have taken a small step toward carnivory must have a higher reproductive value than the plants that did not and thus be represented in greater proportion in the population of the species going forward. There would be no map or plan for the future, no sacrifice now for a reward later, just what works in the present. A botanist looking at the plants in the very distant past would have no clue that in a few million years the descendants would be carnivores. Similarly, looking backward today, the plants can offer us clues to how they became carnivorous, but there will always be some level of uncertainty. We do have one advantage in that carnivorous plants are not inventing new biology.

John DeGreef (1990) summarized in CPN the thoughts on *Cephalotus* evolution prior to 1990. At that time, we did not know *Cephalotus* has a separate lineage going back about 80 million years, which plant order it is in, and certain details of basic leaf development. Now we know that during the Cretaceous geological period dominated by dinosaurs, at some point the “order Oxalidales” consisted of what would have been considered one genus and many species. One of those species was the founder of what we today call the family Cephalotaceae. Because of the difficulty of taxonomically placing families in the Oxalidales and the closely related order Malpighiales owing to a lack of common characters (Stevens 2017a,b) and that these orders and their families arose so

close to the basal Rosid explosion 110 million years ago (Li *et al.* 2019), it is likely at that time the plants were herbaceous and did not have complex leaves. As such, the *Cephalotus* lineage likely did not inherit any specific complicated leaf type. If how it develops its leaves is similar to certain of its relatives, the similarities evolved separately from a similar set of genetic predispositions and environmental challenges.

As we have seen above, it is quite easy for a plant lineage to develop compound leaves from simple leaves. Shifting the balance of the leaf primordia developmental signals in the outer/abaxial direction can result in leaflets piling up on the far abaxial side producing a leaf with a strong rachis containing many leaflets like *Juglans* (walnut), while shifting the balance in/adaxially produces sided palmate leaves like *Acer* (maple) and, in the extreme, peltate palmate leaves like *Oxalis* and *Tropaeolum*. *Cephalotus* went in the same direction as *Oxalis*. *Cephalotus* most likely went from one to three to five leaflets prior to evolving pitchers. Were the leaflets fused like they can be in *Acer* and are in *Tropaeolum* or separate like in *Oxalis*? At some point they had to fuse to make pitchers but there needs to be an environmental reason to do so. *Acer* and *Tropaeolum* do not accumulate water in their leaves. There would be reasons for a *Cephalotus* ancestor not to accumulate water in its leaves unless it was already carnivorous and the water allowed it to capture more prey.

There is evidence that all other pitcher or pitcher-like carnivorous leaves evolved from sticky carnivorous leaves. *Nepenthes* closest living relatives are the sticky leaved *Drosophyllum* and *Triphyophyllum*. *Sarracenia*, *Heliamphora*, and *Darlingtonia* have *Roridula* as a close relative; *Genlisea* and *Utricularia* have *Pinguicula*. The advantage of pitchers over sticky leaves is in rainy environments, the rain will wash prey off the sticky leaves and the mucilage that could trap more. The rainforest sundew, *Drosera schizandra*, in the wild is only a nominal carnivore because of rain (Fleischmann 2011; Fleischmann *et al.* 2018). In addition, it has the problem of “theft” of prey by ants and other animals (Bourke 2006; McPherson 2008). *Cephalotus* today lives in an environment where ants are common and specializes in trapping them (Cross *et al.* 2019). If *Cephalotus* started out as a sticky-leaved carnivore, there would be an advantage evolutionarily to catch the ants that plague sticky-leaved carnivores in rainy locations. But how can that happen in a step-by-step manner where each step is advantageous in the present?

To the extent that ancestral *Cephalotus* leaves developed in a way similar to *Oxalis* with the leaf apexes pointed at the apical meristem, simple shifts in the developmental signaling could easily produce a pitcher-like leaf. First, signaling changes can shift separate leaflets to leaflets fused toward the base. This would be required to construct a pitcher. Second, rather than bending the petiole a full 180°, the plant could have reduced the petiole bend and increased the growth of the most distal leaflet. This would have created a pouch from three leaflets. This developmental shift makes what was the sun side of the leaf, the internal part, while the shade side becomes the outside exposed to the sun. There has to be a very good reason for this shift. It only makes sense if the sun side is the carnivorous surface of the leaf and the plant can trap more prey if the carnivorous side is inside a pitcher.

The development of the *Cephalotus* pitcher lid is similar to the development of the fourth/inner/adaxial leaflet of *O. tetraphylla*. During development, the fourth leaflet of *O. tetraphylla* faces toward the other three leaflets which face toward it. During *Cephalotus* evolution, the leaflets that became the lid appear to have fused separately from the other three leaflets. As far as I can find in the literature, this sort of adaxial/abaxial interaction has not been studied so it could be a coincidence with the two species, or a general principle related to leaflets on the inner/adaxial side of the leaf. The lid created by these adaxial leaflets would only be useful if the whole leaf flips 90° from what was probably the ancestral state.

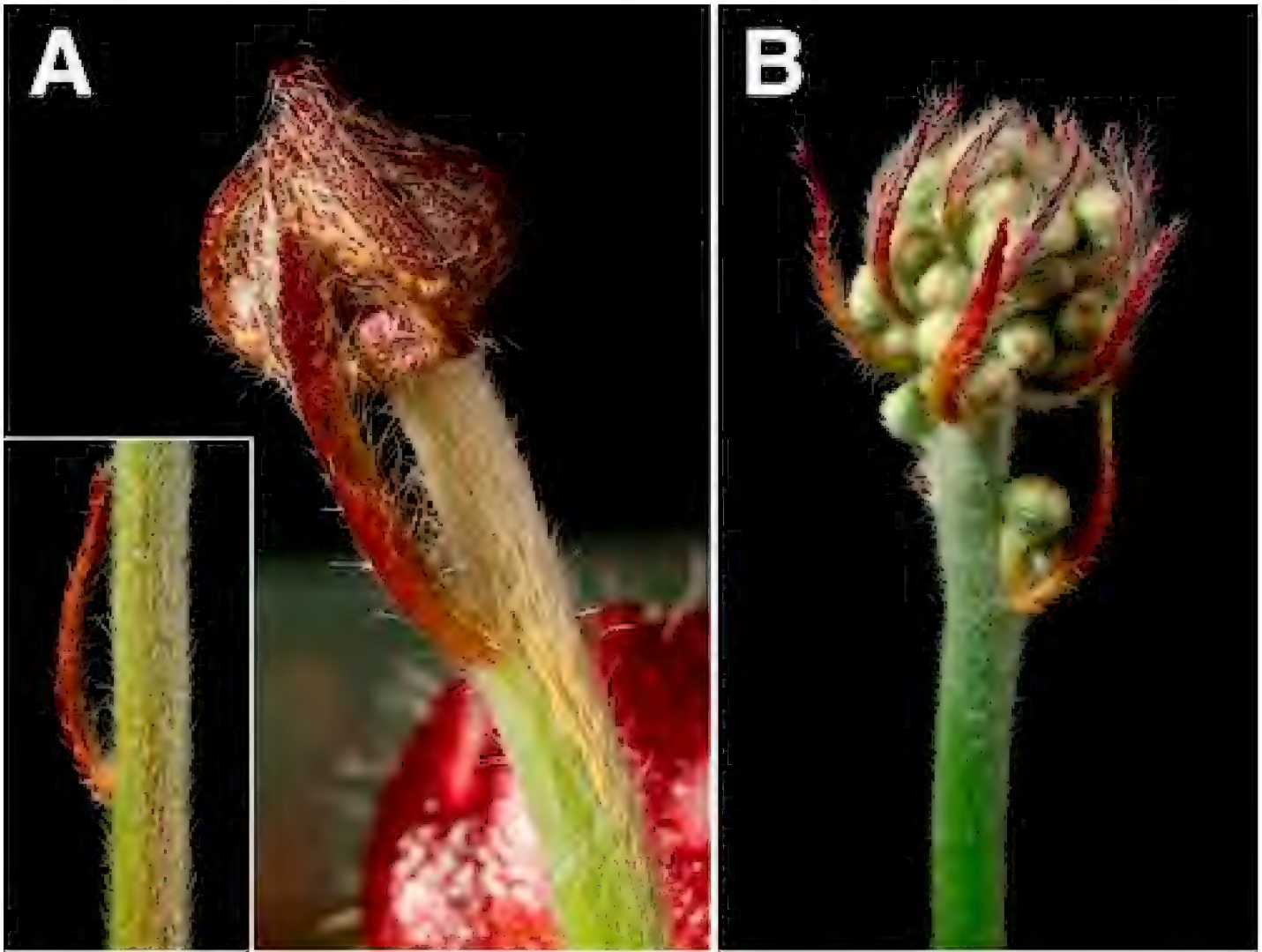


Figure 13: *Cephalotus* flower scapes. The bracts look suspiciously like pitcher front keels. The scape is a rounded “D” shape in cross section. The inset in **A** shows the scape in **A** 14 days later, after the adaxial face turned red. **B** is a different scape but same clone.

The most difficult leaf segment to consider evolutionarily is the front keel. It is long and linear unlike the other developmental domains although they show hints of it centrally. The bracts on flower scapes of *Cephalotus* look suspiciously like the front keel (Fig. 13). In general, bracts are simplified normal leaves and probably use parts of the same genetic program that creates the regular leaves for the plant. Many plants can have bracts on their flower scapes occasionally replaced by incomplete or complete leaves. The bracts on *O. tetraphylla* flower scapes look like the scale-like leaf bases that also make up much of the underground bulb. They do not look like a leaf I observed on an *O. tetraphylla* flower scape with only one leaflet. That leaf was truncate. In *Cephalotus*, the bracts on the flower scapes are most likely present to defend against predation. A keel-like leaf would provide the best protection without interfering with flowering.

The pitcher side wings and “teeth” of the mouth are associated with the lateral developmental domains. The teeth appear to be modified leaf-margin hairs. But the wings are curious because they are internal to the developmental domain. Notice in the photo of the *Cephalotus* seedling in Figure 8 how the lid of this particular plant also shows structures similar to the wings. I like to think that the sticky leaved *Cephalotus* ancestor had heart-shaped leaflets with hairs on the leaf margins similar to *Oxalis*. With heart-shaped leaves, the teeth would have evolved from leaf-margin hairs at the broad distal margin of the leaflets. The wings resulted from fused leaf margins in the notch of the heart. Once there are hairs internally to the leaf in a particular area, evolution has something to work with and can enhance it if it is useful. However, there could be something completely different happening

with the wings. It could simply be an expression of the keel centrally as seen in the intermediate leaf in Figure 9A-B. This could mean an ancestral leaf or the leaflets could have been similar to the bracts and keel.

The pitcher back is the last part of the leaf to complete development. Froebe and Baur (1988) imagined an ancestral leaf for *Cephalotus* with a strong rachis similar to *Vesselowskyia venusta*, an Australian member of Oxalidales family Cunoniaceae (cf. image in Wikipedia), except their drawing shows the two most proximal leaflets fused adaxially. The back of the *Cephalotus* pitcher is analogous to a rachis in the sense that the back spreads the fused leaflet domains in the way a rachis separates entire leaflets. But that does not mean the *Cephalotus* pitcher back is homologous to a rachis in an evolutionary sense. It is extremely unlikely the common ancestor of the Oxalidales was sufficiently specialized to have a rachis. An ancestor in the *Cephalotus* lineage would also be unlikely to have a strong rachis. It would be difficult evolutionarily to get from a leaf as specialized as is the leaf of *V. venusta*, or even *O. tetraphylla*, to a *Cephalotus* pitcher. Irrespective of the history, a concept of what happens with a rachis is occurring late in the development of *Cephalotus* pitchers.

Even if we had a complete understanding of *Cephalotus* leaves, it would not be possible to draw pictures of the ancestral leaves with any confidence. We would know what had to happen over the past 80 million years, but we would not know the sequence of events. At various points there would have had to be one, three, then five leaflets or leaflet developmental domains. At some point before the leaves started to evolve into a pitcher, the plant was most likely carnivorous. At some point three of the carnivorous leaflets had to fuse in order to hold water while the other two fused to create a lid. At some point the leaves became peltate. However, without knowing the sequence of details, we can see how what at first glance is a bizarre leaf, actually results from simple developmental shifts with added ornamentation. Given the millions of years of evolutionary time, the curious ornamentation of prey guides, teeth on the trap margins, and light windows are details that had plenty of time to evolve into their current form.

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SMALL BUTTERWORT (*Pinguicula pumila*) IN ITS NATURAL HABITAT

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Keywords: *Pinguicula pumila*, flower biology, pollination, stigmatic curling.

Abstract: Two wild populations of Small Butterwort (*Pinguicula pumila*, Lentibulariaceae) were studied during its 2019/2020 late autumn–spring flowering season in Palm Beach County, Florida. The rare yellow-flowered form known primarily from Southwest Florida turned up in East Florida. Except possibly for 19th century literature we were unable to examine, stigmatic curling in response to touch is first reported for *Pinguicula*. Diverse Dipteran and Hymenopteran floral visitors were observed. Previous indications that spontaneous self-pollination is rare to none in this and related species, especially with reference to cultivated plants, were consistent with our results using insect exclosures on wild plants, whereas open-pollinated flowers made fruits and seeds abundantly. In our area the known populations are all spotty and small, in wet-then-dry disturbed habitats.

Introduction

South Florida is a great place for native carnivorous plants, with sterile soils, extensive wetlands, and insects aplenty year-round. Here live several species of *Drosera*, *Pinguicula*, *Utricularia*, and, marginally, *Sarracenia*. The tank bromeliad *Catopsis berteroniana* hosts bacterial symbionts as digestive aids. The present study is a profile of one of the prettiest and most curious local insectivores, Small Butterwort, *Pinguicula pumila* Michx.

Distribution and Habitats

Butterworts, comprising the genus *Pinguicula*, number debatably around 75 species from Canada to Chile, and around much of the globe mostly in North Temperate regions (Legendre 2000). Six live in Florida, comprising a single clade (Shimai *et al.* 2007). *Pinguicula pumila* resembles the other Florida species by having a nearly round floral tube that closes and nods at night, although the plants are distinctively tiny. The basal rosettes are often around 2-3 cm across, with the taller floral stalks rising to about 7-12 cm bearing flowers with the petals spread to about a cm.

The overall range of *Pinguicula pumila* is the Southeastern Coastal Plain from the Bahamas to Texas, including most of Florida. In South Florida, *P. pumila* blooms winter through early spring on seasonally inundated and later drying, sunny to lightly shaded, muddy, sandy, or marly habitats. Although specific pH data are mostly lacking, herbarium label data suggest broad tolerances in that regard.

The wet-then-dry habitats are varied, including pine woods, ditches, and shores. Moist pathways, roadsides, and power lines dominate specimen labels in the University of South Florida Herbarium. This preponderance of disturbed rights-of-way begs the question of management practices, especially the relationship of Small Butterwort with glyphosate-based weed control, prescribed burning, roto-chopping, and feral hogs. Disturbance appears to favor the species.



Figure 1: Habitat of *Pinguicula pumila*. Cypress Creek site near Jupiter, Florida.

The two populations we studied late autumn through spring 2019/2020 are in and adjacent to semi-neglected dirt roads in low wet slash pine woods in Palm Beach County on the Florida southeastern coast. One patch is in the Pine Glades Natural Area west of Jupiter, Florida, the other a few miles farther east, occupies similar habitat in the Cypress Creek Natural Area (Fig. 1), and was the site of most of our efforts. We are aware of three additional nearby patches, two in and adjacent to disturbed dirt roads through low pine woods. The third occupies nearly bare sandy soil upturned by feral hogs.

In our area, Small Butterwort is usually mixed with other moisture-loving insectivores, *Drosera capillaris* and *Utricularia subulata*. Locally present also, if not in the immediate company of *P. pumila*, are *Pinguicula caerulea* and *P. lutea*, both larger in all dimensions.

Prey Capture

Most prey are tiny, rapidly degraded, and hidden under the curling leaves. We have observed small Dipterans, springtails, what appear to be minute beetles, and ants. Curiously common on the sticky leaves are planthoppers, *Delphacodes puella*, a widespread herbivorous species. These, perhaps due to size and strength, frequently evade capture by leaping away upon disturbance. It is unclear if their presence is random, or perhaps due to some form of attraction. Mary Treat (1876) suspected slash pine pollen to help feed the foliage.

Flower Colors

The most salient feature of *P. pumila* is the mix of its floral colors intermixed in any given patch. In our experience, white and violet are almost always together, sometimes on the same rosette. The



Figure 2: **A:** Yellow *Pinguicula pumila* flower. **B:** *P. pumila* palate in violet flower.

patch on the soil upturned by hogs is completely white-flowered although we are not suggesting any connection between the hogs and flower color. The flowers usually have yellow throats and reddish nectar guides leading into the spur. Gluch (2005) listed color variations. Flowers of many plant species change color, presumably to signal pollination status to pollinators. A prominent Florida example is Jamaica-Caper (*Quadralla jamaicensis*) where the corollas transform from white to violet. In *P. pumila* marked and monitored uncultivated flowers likewise sometimes change from white to violet. The violet coloration grades from barely perceptible to deep and rich. Many flowers remain white through their entire life.

A rare bright yellow variant (Fig. 2A) is best documented in southwestern Florida. We found bright yellow, white, and violet blossoms all together at the Pine Glades site. The yellow variant has been recognized previously as *P. pumila* var. *buswellii* Moldenke. Given its mingling among the white- and violet-flowered individuals, there is no basis for taxonomic recognition except arguably as a “forma,” which we regard as pointless. Other botanists, for example Wunderlin *et al.* (2020) have placed var. *buswellii* in synonymy where it belongs.

Fleischmann (2016) suggested that, because *Pinguicula* offers false pollen on the fuzzy yellow palate (Fig. 2B), pollinators may learn to avoid flower colors associated with false promises while remaining willing to try other colors on the same species, as a frustrated gambler may try different slot machines in the same casino. We wonder alternatively if the different-colored flowers “suggest” the diverse colors of different nearby rewarding species. There are similar-sized, white (e.g., *Viola lanceolata*, *Mecardonia acuminata*), violet (e.g., *Lindernia grandiflora*, *Sisyrinchium angustifolium*), and yellow (e.g., *Utricularia subulata*, *Xyris elliottii*) flowers around to share visitors. We mention the analogous flowers as general examples of plausibility, not to suggest one-on-one mimicry.

Some species of *Pinguicula*, perhaps all, offer true rewards. Lustofin *et al.* (2019) documented nectary hairs in *Pinguicula* floral spurs, although they did not check *P. pumila*. A tiny insect visitor we photographed in a yellow *P. pumila* flower was eating or nuzzling knob-tipped hairs in the floral tube at the time of our photo. Knob-tipped hairs from *P. pumila* are illustrated in Wood & Godfrey (1957).

Floral Structure and Function

The flowers rise singly on one to several delicate scapes a few cm above the rosette (Fig. 3). The maturation time for a scape and its flower is several days, and the mature flower likewise persists several days. The tubes are usually, but not necessarily, upright at times of visitation. We find most flowers to open 10-11 AM EST and to close and nod late afternoon well before dark, not opening or closing in unison. Weather makes a difference. In other Florida *Pinguicula* species, Molano-Flores *et al.* (2016) found unpollinated flowers to last longer than pollinated ones.

The flowers are tubular and provided with a spur. The corolla tube has on its “floor” a pronounced outgrowth, the palate which is a hairy yellow ridge sloping down and inward toward the stigma and partly blocking entrance to the tube.

Wood & Godfrey (1957) regarded the palate as a “foothold” for pollinators. It presumably has an “advertising” function, given its bright yellow coloration. False-anthers and yellow floral decorations are common in the plant world. Additionally, the palate may block unauthorized insect visitors (see footage suggestive of this in the video link provided below), may help guide welcome visitors inward, and may participate in the physical dynamics of floral shape during insect visitation.

In a flower opened on its side with the pedicel at the “top” and the palate at the “bottom,” the palate is visible lengthwise, with the pistil and stamens deeper in the flower. The globose ovary is sessile where the pedicel joins the tube. From the ovary a short style holds the large flat stigma as a ramp having its top (toward the pedicel) deeper in the tube than its base on the floor of the tube behind the palate (Fig. 4).

Looking into the mouth, the palate greets the eye end-on (Fig. 4 righthand views, Fig. 2). Behind it the tilted stigma blocks most of the tube. The top of the stigma (2nd lobe) almost matches in shape the opening around and above it. At the floor of the tube behind the palate the stigma covers the two anthers (Fig. 5A) and prevents access to the spur.



Figure 3: White *Pinguicula pumila* flower on scape.

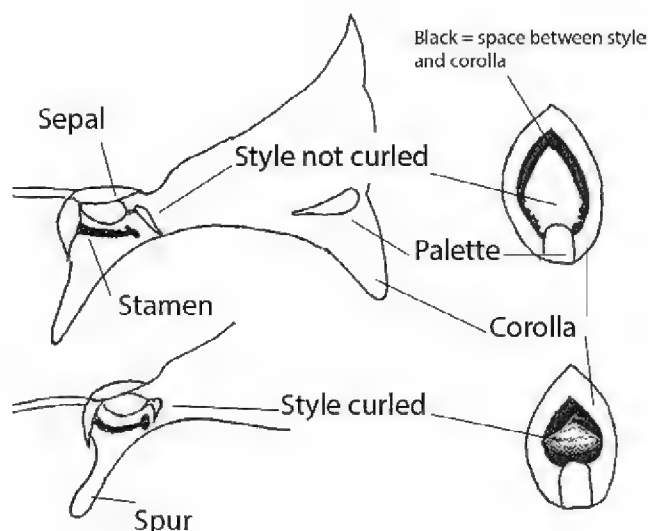


Figure 4: *Pinguicula pumila* flower diagram (cross-section from side) showing uncurled and curled condition of stigma.

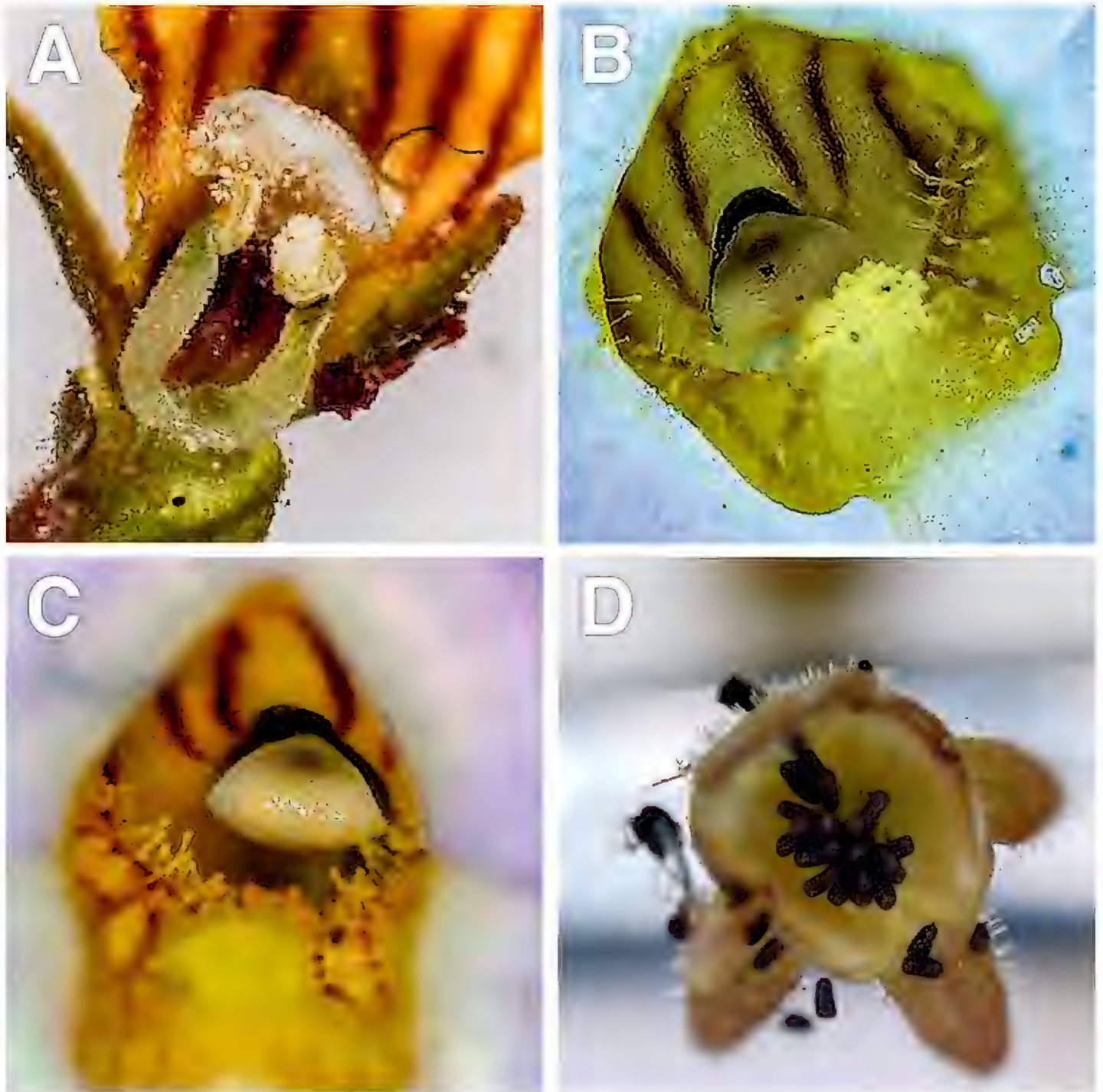


Figure 5: **A:** View of *Pinguicula pumila* stamens from beneath (lower corolla lip removed); **B:** stigma not curled; **C:** stigma curled; **D:** fruit (cut open) with seeds.

Stigmatic Curling

In related *Utricularia*, the stigma curls upon physical stimulation. Newcombe (1924) looked for similar sensitivity in *Pinguicula* but failed to find it in species he examined, not including *P. pumila*. We have found the stigma sensitive in *P. pumila*. Probing the flower with a false proboscis, for instance a tiny stem, causes the stigma base to curl back and inward, opening the door to the spur and exposing the anthers to insect contact. The movement happens within seconds of contact, or repeated contacts, and the movement lasts about 1 or 2 seconds. The uncurled and curled stigmatic positions appear in Figures 5B-C. Wild plants examined undisturbed commonly have curled stigmas, while many others have the stigmas uncurled. If and when or under what circumstance they may uncurl is not established.

Floral Visitors

Wood & Godfrey (1957) and Molano-Flores *et al.* (2018) determined other Florida *Pinguicula* species to be pollinated mostly by Hymenopterans. Using video cameras, in *P. pumila* we recorded numerous floral visits where insects entered the floral tube in addition to several non-penetrating “inspections” or perhaps would-be visits thwarted by the palate. Visitors witnessed entering the flowers are diverse, including wasps and Syrphid flies. Visitation is displayed at <https://vimeo.com/399208537>. An odd floral guest was the tiny Hymenopteran mentioned above in connection with the corolla hairs. Under natural conditions the plants regularly produce abundant capsules and seeds (Fig. 5D), although many flowers end up seedless, and many rosettes of this delicate species decline before reproductive success.

Self-Pollination

The stigma curling toward the anthers, even if the receptive surface does not contact anthers directly, hints at potential for self-pollination. Merilaun (1895) with reference to other *Pinguicula* species described stigma curling as a response to age, and suggested the movement to assure pollination. Citing multiple 19th Century authors reporting curled *Pinguicula* stigmas, Willis & Burkill (1903) reported seeing pollen tubes from the anthers entering the curled stigma in sectioned material of *P. vulgaris*. If age-related (or otherwise induced) curling leads to selfing as Marilaun and Willis & Burkill perceived over a century ago, stigma curling as a result of insect visitation could conceivably cause selfing in *P. pumila*, although that notion has complexities:

Wood & Godfrey referring to all the Southeastern *Pinguiculas*, and later Fleischmann (2016) determined *Pinguicula pumila* to be self-compatible, and the latter author found *P. pumila* not to self-pollinate spontaneously in cultivation. We have seen the same failure to form capsules on two flowering cultivated rosettes. Similarly, Molano-Flores *et al.* determined *Pinguicula ionantha*, *P. planifolia*, and *P. lutea* (see also Primer 2016a) to be self-compatible yet free of spontaneous self-pollination or very nearly so. Primer (2016b) speculated that an insect-visitor might cause selfing along with whatever outside pollen it delivers in the species she studied, not *P. pumila*. This would make sense, given the massive numbers of seeds produced requiring enormous numbers of pollen grains, debatably more than floral visitors are likely to deliver.

Our results echo our predecessors that spontaneous self-pollination is minimal at best. At the Cypress Creek site, we excluded flying visitors for 4-6 weeks from 16 marked rosettes under small screen tents affixed to the ground with nails. None of the rosettes had open flowers, post-opening flowers, or maturing capsules at the time of covering. The rosettes were allowed to flower under the tents, most rosettes producing numerous blossoms during the study period. The tents were placed on different days within the first two weeks of February and monitored until the time of this writing in late March. Of these, one flower produced a dehiscent seed-bearing capsule. A single instance could be caused oddly, perhaps even by insects crawling under the tent, although crawlers would have to run the gauntlet of the sticky leaves and scape.

Wondering if probing the flowers in the fashion found to trigger stigmatic curling might boost self-pollination, pre-anthesis plants were allowed to flower under seven screen tents with each flower probed upon opening. This crude simulation of insect visitation resulted in one flower producing seeds, not a discernable boost. It is impossible to know if the ostensibly probe-induced self-pollination resulted from stigmatic curling, or from self-pollen clinging to the probe, or otherwise.

In short, spontaneous self-pollination is probably unimportant as a back-up means of reproductive assurance, given its reluctance to occur, and given that in open-pollinated flowers insect visitations are common, as are fruit and seed production. A possible consequence of self-pollination in general is the conferred ability of lone plants to found new populations. The scarcity of selfing in *P. pumila* might coincide with the scarcity of isolated patches in seemingly suitable habitats.

Dispersal

In our area the patches are spotty, small, and widely scattered relative to what seems to the inadequate human eye to be suitable habitat, perhaps the outcomes of individual seed releases, although unknown ecological constraints probably matter too. The dust-sized seeds undoubtedly disperse sometimes by wind and on creatures. Locally the plants favor rough dirt roads traversed by maintenance crews, hikers, hunters, equestrians, and abundant hooved wildlife, all suspected agents of seed dispersal.

Water movements certainly relocate seeds in this immersion-prone species. The patch borders reflect the boundaries of large seasonal puddles. During the 2019/2020 winter and early spring the Cypress Creek patch borders morphed like an amoeba as the wet-dry and sun-shade patterns changed, older rosettes faded out while replacements popped up outside the original patch footprint. As conditions became seasonally hotter and drier, the largest and most robust individuals were in shade with violet-colored flowers more abundant than elsewhere. We were unable to detect any form of vegetative propagation and dispersal.

Summary

Pinguicula pumila has largely fallen between the academic cracks. Within the scope of our study it forms small patches in disturbed sites prone to seasonal immersion followed by drying, the rosettes tolerating both extremes. Among the prey, planthoppers visit the leaves, frequently able to leap free. White and violet flowers are almost always together, even on the same rosette, and some white flowers become violet. The yellow-flowered variant occurs freely mixed with rosettes bearing white or violet flowers. The flowers are complex. The stigma hides access to the floral spur and to the anthers until physical contact triggers curling. Consistent with prior reports, the species is self-compatible yet disinclined toward spontaneous self-pollination. Our encounters with curling stigmas are more consistent with *Utricularia* and with 19th Century reports on *Pinguicula* than with contemporary research on the other Florida species. Floral visitors are varied, including Dipterans and Hymenopterans. Capsules and seeds are plentiful under open pollination in natural habitats. A one-season study raises more questions than it answers, some of them beyond our technical equipment and ability. Suggested further research includes broadened data on the relative importance of self-pollination and factors influencing it including insect visits, stigmatic status before and after visitation, stigmatic dynamics in this and related species, pollen loads on visiting insects, population genetics and gene flow, and demography of the small isolated patches.

Acknowledgment: Appreciation is extended to Frank Griffith, Environmental Program Supervisor, Palm Beach County Environmental Resource Management, for discussion of the project, project-specific vehicular access to an otherwise gated road, and permission-marker on car to park at the main study site. Rogers holds a Palm Beach County Scientific Research Permit extending to the Cypress Creek and Pine Glades Natural Areas.

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EVIDENCE FOR MOTILE SUCTION TRAPS IN *UTRICULARIA WESTONII* FROM *UTRICULARIA* SUBGENUS *POLYPOMPHOLYX*

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Abstract: Here we report that traps of *Utricularia westonii* from *Utricularia* sect. *Tridentaria* are working with a very effective suction mechanism, which was revealed and recorded during feeding experiments with cultivated specimen.

The bladderworts (*Utricularia* spp., Lentibulariaceae) comprise more than 240 species with several life-forms (Fleischmann 2015). It is generally believed that they capture their prey with leaves that are modified into suction traps, commonly termed “bladders”, which are the fastest trapping devices among carnivorous plants (Lloyd 1942). Suction is rendered possible by a complex interplay of functional-morphological, physiological and mechanical prerequisites (reviewed by Poppinga *et al.* 2016). Water pumps shift water from the trap lumen to the exterior, thereby generating a sub-ambient pressure inside the traps. The trap walls are elastically deformable and thereby store elastic energy. Furthermore, the traps are closed watertight by a thin and flexible trapdoor, which can swiftly open and close after touch by prey to allow the traps to perform their suction strike.

There has been some debate recently whether traps of phylogenetically early branching terrestrial or affixed aquatic species from *Utricularia* subg. *Polypompholyx* meet the above criteria, i.e. if they possess motile suction traps, or if they work as non-motile eel traps similar to those of *Genlisea* (Fleischmann *et al.* 2012). Especially *U. multifida* (*U.* sect. *Polypompholyx*) has been investigated in this respect: although Lloyd (1942) reported that the traps are motile, later analyses by Reifenrath *et al.* (2006), finding that they possess exceptionally thick trapdoors, and Westermeier *et al.* (2017), which were unable to record suction events in laboratory experiments, have led to speculations that they might be non-motile on the contrary. Plachno *et al.* (2019) attributed the traps of *U. multifida* and *U. westonii* (*U.* sect. *Tridentaria*) to possess the structural prerequisites for suction, but could not definitively prove this trap functioning experimentally. *Utricularia tenella* (*U.* sect. *Polypompholyx*) has never been investigated in this respect. At least for *U. westonii*, which is endemic to Cape Le Grand National Park, southwestern Western Australia (Fig. 1A,B), the exact trap functional principle can be considered as revealed with this short communication.

Marco Pezzotta grew this species from November 2016 until March 2020 following a methodology proposed by Spence (2005). The seeds of this annual species, which grows during winter, were originally obtained from Allen Lowrie. The plants were cultivated outside for their whole life cycle in San Salvo (CH), Italy, which is characterized by a Mediterranean climate with winter temperatures never below 0°C. The sowing was carried out in late summer on a substrate consisting of peat and fine quartz sand in a ratio of 40/60 and with a superficial layer of sand only. The pots have been placed in a container, with a level of demineralized water slightly lower than the surface of the substrate. Then the pots have been covered with a transparent lid to avoid rain and to limit evaporation. During germination, which can take from a few weeks to a couple of months, direct sunlight illumination is not required. Once the seedlings had anchored to the substrate with their rhizoids, after

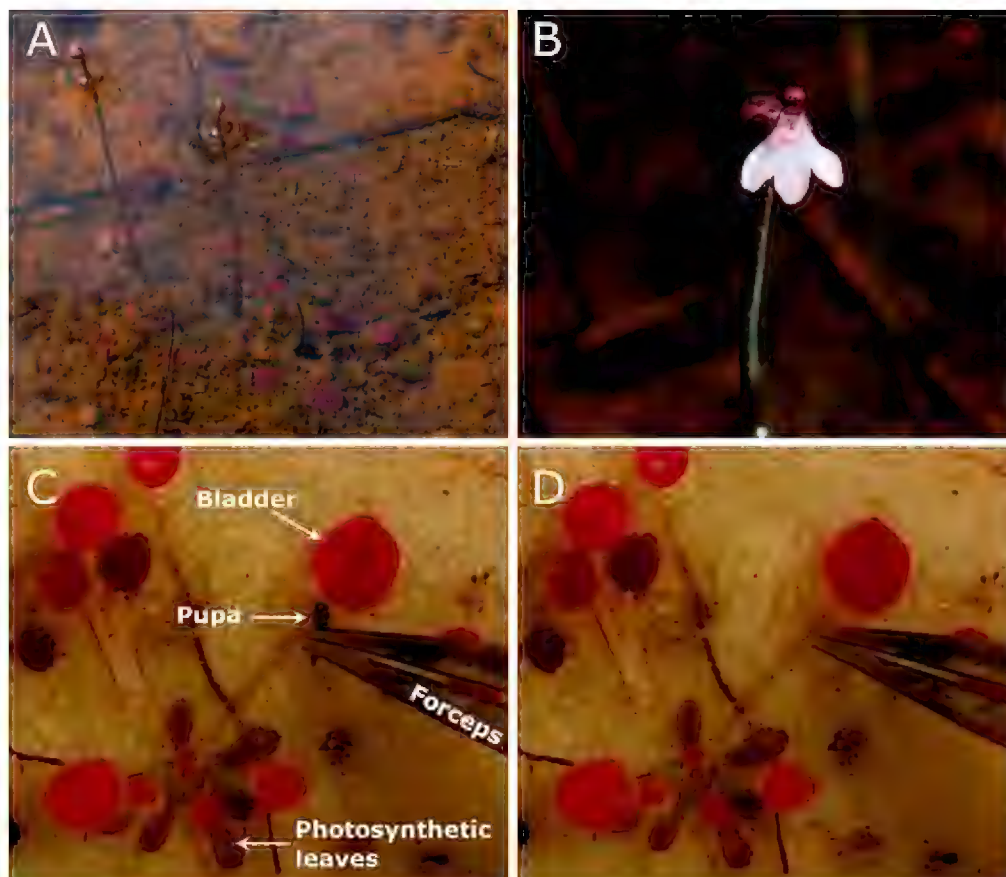


Figure 1: *Utricularia westonii*. A) Submerged plants in the Cape Le Grand National Park. B) Flower. C) Feeding of a cultivated plant with a dipteran pupa. The pupa is handled with forceps and brought to the entrance zone of the trap. D) The pupa has been sucked into the trap. The two frames C) and D) are from a movie, which can be seen on Marco Pezzotta's YouTube channel (FreakyPlants Marco Pezzotta), or be obtained from the authors upon request. The movie was recorded with 30 fps, the time duration between the two frames hence is ~33 ms. However, the real duration of suction is likely to be even faster. The movement of the lateral trap walls is not visible in this recording. Photos A, B by A. Fleischmann, C, D by M. Pezzotta.

reaching about 3-4 leaves, the water level was raised about 2-5 cm above the substrate in order to submerge the plants. The water in which the plants were grown contained crustaceans such as copepods and ostracods for allowing the plants to capture prey essential for growing and flowering. The flower scapes began to emerge in spring and, when possible, the plants were cross-pollinated. In all the other cases, plants were allowed to self-pollinate. Both procedures led to the production of fertile seeds.

Marco was able to film suction in his cultivated plants with a mobile phone camera (Xiaomi Redmi Note 5) (Fig. 1C,D). A video of the suction action can be seen on his YouTube channel (FreakyPlants Marco Pezzotta, <https://www.youtube.com/watch?v=UOKThdl1JFg>), or be obtained from the authors upon request. The video shows that suction is triggered during feeding with an immobile dipteran pupa (3.1 mm length on average, $n=5$), which is handled with a pair of forceps. Indeed, this is a very elegant method of feeding prey to the traps (3.4 mm length on average, $n=5$, without appendices). Marco regularly observed suction actions during the feeding procedures, so that the suction event presented in Figure 1C,D (and in the respective video) is not an exception. Indeed, *U. westonii* is described to possess trigger hairs on its trapdoor (Płachno *et al.* 2019), which are responsible for trap activation upon touch in bladderworts in general (Lloyd 1942). The swift displacement of the dipteran pupa between two frames of the recording (relating to a duration of ~33 ms [milliseconds] according to 30 fps recording speed) is indicative of a rapid suction action. However, we believe that the timescale is presumably even (much)

smaller, as suction in *Utricularia* can be ultra-fast: about 9 ms were measured in aquatic *U. australis* by Poppinga *et al.* (2017). Due to the triangular shape of the *U. westonii* trap (as seen in transverse section) (Taylor 1989) and the orientation of the recording camera, the movement of the lateral trap walls is not visible. The trap motion can be resolved in full temporal resolution only with adequate high-speed camera setups and remains an interesting aspect for future approaches, e.g. for studying fluid dynamics.

Until now, we do not know which prey is being caught by species of *Utricularia* subg. *Polypompholyx*. Probably, the conspicuous trap shapes in combination with the terrestrial/affixed aquatic lifestyles represent adaptations to capture shelter-seeking crustaceans like small ostracods. We also do not know if these traps are capable of sucking spontaneously, i.e. without being triggered mechanically by prey. This autonomous behaviour is reported from many aquatic and non-aquatic species (Vincent *et al.* 2011; Westermeier *et al.* 2017) and helps these plants to accumulate digestible biomass like algae in their traps (Koller-Peroutka *et al.* 2015). In conclusion, many functional aspects remain unclear for these phylogenetically early branching species.

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LITHOPHYTIC CULTURE OF MEXICAN *PINGUICULA*

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Abstract: Attempts to replicate in cultivation the natural lithophytic growth habit of many Mexican *Pinguicula* seem to have taken off in popularity in recent years. Herein I describe my own experience with this technique and the approaches that I have found to be successful in the long-term.

Introduction

Lithophytic plants grow in or on rock. Broadly speaking, they may be facultative (meaning they may also occur in other substrates) or obligate (meaning they only grow on rock). Quite an impressive number of Mexican *Pinguicula* demonstrate lithophytic growth tendencies in habitat; the sight of dozens of specimens clinging vertically to the surface of sheer limestone walls is wonderful! Naturally, horticulturists have attempted to replicate this mode of growth in cultivation, and many have achieved very impressive results. I have experimented with growing a variety of Mexican *Pinguicula* on rocks for several years and have come up with a list of factors that I believe are crucial to success with this technique. By no means are my *Pinguicula* rock plantings the most spectacular out there, but I do hope that my experiences will be helpful to all those who wish to create one!

Growing *Pinguicula* on rocks

Lithophytic Mexican *Pinguicula* are frequently found growing in crevices of limestone or gypsum where water can accumulate (Mata-Rosas *et al.* 2020). To replicate this effect in cultivation, the rock selected for the substrate should be porous and allow for water to wick upwards toward the plants' roots (Fig. 1). Vesicular volcanic rocks, especially pumice and scoria, are ideal for this purpose. These rocks are pitted with numerous cavities that facilitate water retention and provide

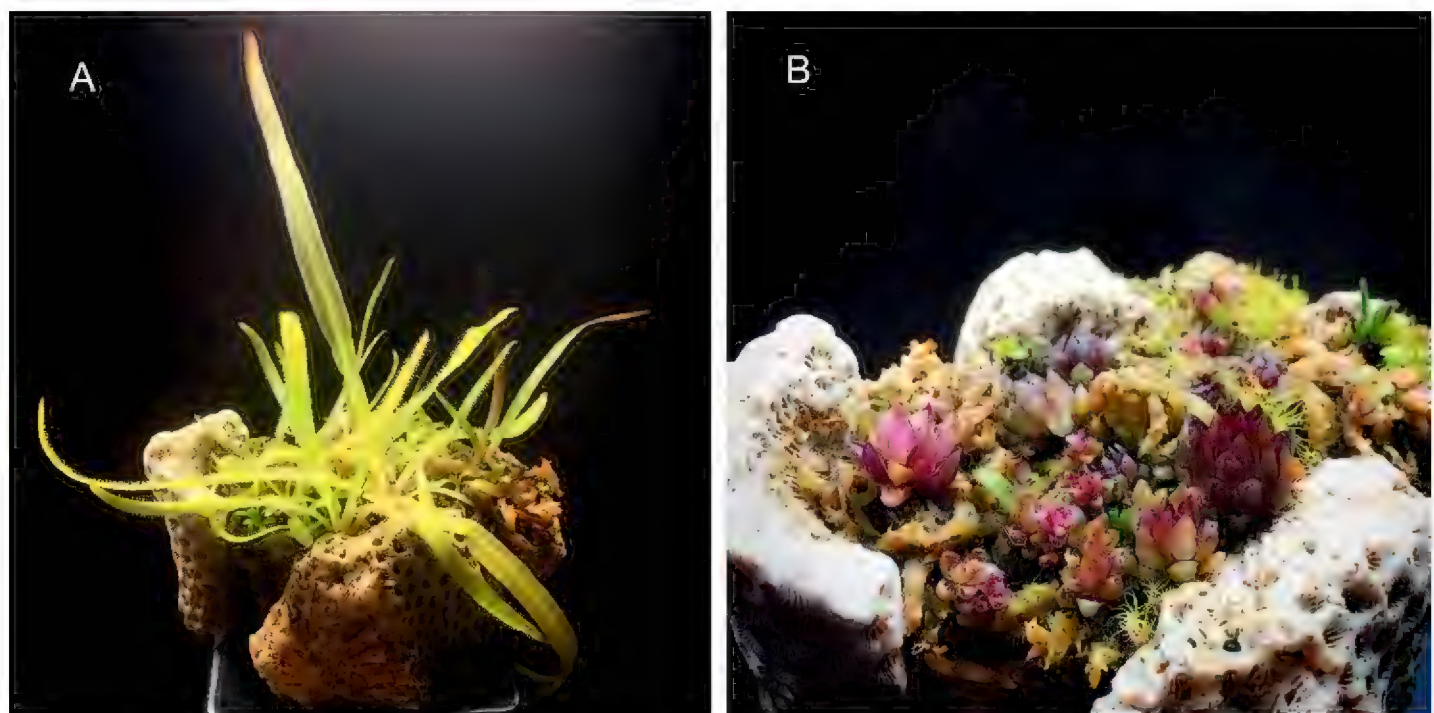


Figure 1: *Pinguicula calderoniae* (Llano del Conjeo, San Luis Potosí) growing on chunks of old coral paperweights glued together with epoxy resin. (A) Plants in vegetative growth. (B) Winter succulent rosettes.

convenient little crevices for plant roots to establish themselves. Pumice has smaller, more numerous vesicles, while scoria is denser and has larger vesicles with thicker walls. I have observed that pumice tends to wick water more reliably, but they are both very suitable substrates. Since growing *Pinguicula* on rocks is, at heart, an artistic endeavor, be sure to select a rock that you find aesthetically pleasing with indentations or pockets where plants will fit. If no such crevices are present, feel free to take initiative and drill holes. The rock should not be too tall, otherwise water may not wick upward efficiently. Also be sure that the rock has a somewhat flat base or is stable when left up by itself. It would be embarrassing for your brand-new planting to suddenly tip over! Sit the rock in a shallow tray of water overnight to ensure that the location where you want to place plants receives sufficient moisture.

It is certainly possible to grow *Pinguicula* on non-porous stone. However, to ensure that the plants do not desiccate, they will either have to be watered very frequently (perhaps even multiple times a day), or a wick will have to be provided to draw up water to the root zone. I recommend the wick approach. I would not trust myself to remember to water the plants frequently enough without one.

With your favorite rock selected, you can now begin adding plants. Wash the old media from the roots and maneuver the plant into the proper hole or crevice. Fortunately, most Mexican *Pinguicula* have very little in the way of roots so this should not be too difficult. I have found that partially stuffing the hole with a small amount of organic matter like *Sphagnum* moss helps anchor the plants. Once all the plants are placed, place the rock in a shallow tray of distilled or deionized water and grow the plants as you would in standard pots. Avoid tap water high in dissolved solids—the minerals will form crusty, unpleasant deposits on the rock. During the growing season, the water level should be kept below the plants' leaves but high enough so that the roots receive moisture. The water will likely have to be periodically replaced to remove algal growth. High amounts of light are necessary to have the plants look their best and prevent the growth of mold; rock plantings are easily managed on very bright windowsills or under high-powered LEDs or fluorescent bulbs. If you live in an area with very intense summers, be careful to avoid placing the rocks in direct sunlight for too long, especially if you are using darker rocks such as basaltic scoria. They can heat up very quickly and bake your plants.

In terms of plant selection, the species that frequently occur as lithophytes such as *P. gypsicola* and *P. agnata* are obvious candidates. However, I have also been successful with species that tend to grow in mosses or as epiphytes in tropical oak or pine forest, including *P. laueana* (Fig. 2) and mem-

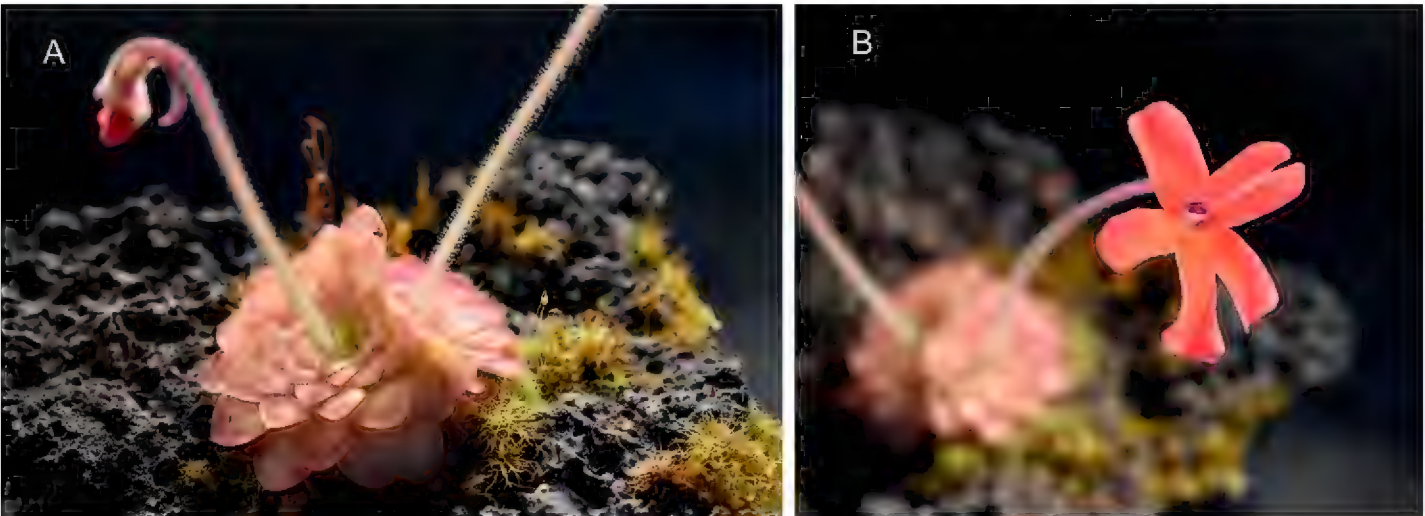


Figure 2: *Pinguicula laueana* is quite at home growing on scoria. (A) Fresh rosettes of carnivorous leaves produced in spring. (B) This species is often noted for its brilliant red bloom.

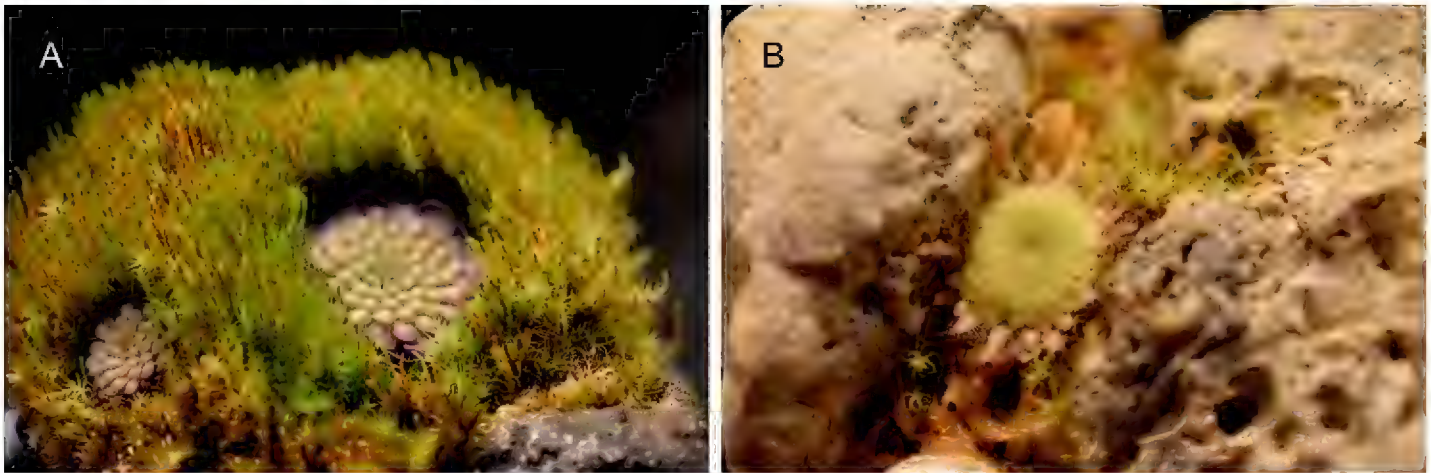


Figure 3: Winter succulent rosettes of Mexican *Pinguicula*. (A) *Pinguicula cyclosecta* grown on scoria. (B) *Pinguicula gypsicola* grown on limestone.

bers of the *P. moranensis* complex. My perusals of other growers’ plantings also indicate success with even inhabitants of tropical rain or cloud forests like *P. gigantea*. It appears that most, if not all, Mexican *Pinguicula* are highly amenable to this form of culture, so do not hesitate to try it out!

Correct managing of the plants’ annual winter resting period is critical to maintaining rock plantings long-term (Fig. 3). As with plants grown in traditional media in pots, water should be greatly reduced when the plants begin replacing their carnivorous leaves with succulent ones in the autumn. This should begin to happen when a reduction in photoperiod is observed. If you grow your plants under artificial lights all year, you may wish to periodically adjust the timer to approximate sunrise and sunset times. Species like *P. medusina* that grow in more xeric, arid habitats (Ruiz & Studnika 2000) are particularly sensitive to rot during their resting period and should be kept completely dry. Water should only be supplied again once the plants begin producing carnivorous leaves.

Over time, it is very likely that your rocks will come to be covered in a thick layer of moss (Fig. 4). I periodically trim and remove moss to prevent suffocation of the *Pinguicula* rosettes but otherwise leave it alone. The moss layer is very effective at wicking water and will ensure that the surface of the rock is permanently moist, so long as the water level is maintained. The moss can also serve as a convenient propagation mat if you wish. *Pinguicula* leaf pullings, especially with succulent leaves, are a well-documented and effective method to vegetatively propagate plants. Pullings that I have inserted into the moss covering my rock plantings have had high strike rates.

I mentioned previously that growing *Pinguicula* on rocks may be considered an artistic endeavor. I say this because there is really no advantage to this mode of culture over traditional media and pots other than the aesthetic aspects. There do appear to be some draw-



Figure 4: *Pinguicula rotundiflora* (Aramberri, Nuevo León) nestled in a moss-covered piece of scoria.



Figure 5: Assorted Mexican *Pinguicula* growing on chunks of volcanic scoria. Their colorful appearance almost reminds me of rock candy. (A) *Pinguicula rectifolia*. (B) *Pinguicula cyclosecta*. (C) *Pinguicula rotundiflora* (Aramberri, Nuevo León) and *P. agnata* “Red Leaf.” (D) *Pinguicula* ‘Aphrodite’ and *P. rectifolia*. (E) *Pinguicula esseriana*.

backs to lithophytic culture—the plants tend to be a bit smaller, most likely due to limited space, and rock plantings are far less space-efficient than pots. That said, *Pinguicula* rock plantings are a wonderful way to create an attractive, relatively low-maintenance display (Fig. 5).

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GREEN ANOLES AS *SARRACENIA* POLLINATORS?

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In the September 2019 issue (CPN 48(3): 136), I reported seeing a female Green Anole (*Anolis carolinensis*) drinking nectar from the lips of *Sarracenia alata* pitchers. As I stated then, “I have witnessed Green Anoles on top of *Sarracenia* quite frequently, and even seen them grab flies that are attracted to the plants. I’ve seen the anoles down inside the plant, seemingly hunting just like the tree frog. However, I have also found anole skeletons inside the “stomach” of some of these pitcher plants. I guess they get stuck sometimes.” I went on to report my findings and video of a female Green Anole drinking the nectar from the lips of *Sarracenia alata*.

This spring, however, I witnessed a male Green Anole licking the pollen from inside the flower of *Sarracenia leucophylla*, a carnivorous pitcher plant from the southeastern United States (Fig. 1). He was just as aggressive about licking up this pollen as the female was about drinking the nectar. I have posted two videos from different days of the male anole licking the inside of the flowers. I know that the flowers are situated to be pollinated by specific insects, but as I watched him crawl over and through the flower, I began to wonder if he could be helping in pollination as well.

Green Anole licking pollen from a pitcher plant flower:

<https://youtu.be/X8njx4Aw9nM>

https://youtu.be/_vJ8eEtk1lw



Figure 1: Male Green Anole licking pollen from the flower of *Sarracenia leucophylla*.

EDUCATION CORNER: ICPS PHOTO CONTEST

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Despite our 2020 biennial conference in Japan being delayed due to COVID-19, we still held a photo contest this year that was curated by Kenny. Our judges were Artists Mindy Lighthipe, Jeremy Miklas, and TIES director Bertha Vazquez.

- Mindy Lighthipe draws and paints the beauty of nature. She believes in protecting the earth and does so by educating people through her art. Her goal is to record the earth's species in the 21st century and educate people to preserve it. <https://www.MindyLighthipe.com>
- Jeremy Miklas is an artist who owns and operates Vivid Buffalo, a creative services company offering a wide range of business needs and custom art needs. He designed all of the carnivorous plants and their prey which were used in our infographics and coloring sheets. <https://www.vividbuffalo.com/>
- Bertha Vazquez is the director of the Teacher Institute for Evolutionary Science, a non-profit foundation passionate about helping teachers explain evolution in an effective and engaging way. <https://www.tieseducation.org>

We had over 200 entries! Your enthusiasm and passion for carnivorous plants is inspiring. Thank you to everyone who participated.

Winners received a 1-year membership to ICPS.



Category 1: Portraits of Carnivorous Plants (a single plant or collection). Winner Boaz Ng (Australia) – *Drosera auriculata*.



Category 2: Carnivorous Plants in the Wild (photos taken of plants in their natural habitat). Winner Trey Hale (United States) – Frog caught in Venus flytrap.



Category 3: People and Plants (Wacky or serious photo of carnivorous plants and the people who love them). Winner Julien Baruch (USA) – *Sarracenia flava* with a hooligan fluttering about.

NEW CULTIVARS

Keywords: cultivar, *Pinguicula* ‘Eye Spy’, *Sarracenia purpurea* f. *luteola* ‘Super-duper’, *Heliamphora* ‘Cyclops’, *Dionaea* ‘Stove Fire’.

Abstract: Four new carnivorous plant cultivars are named and described: *Pinguicula* ‘Eye Spy’, *Sarracenia purpurea* f. *luteola* ‘Super-duper’, *Heliamphora* ‘Cyclops’, *Dionaea* ‘Stove Fire’.

Pinguicula ‘Eye Spy’

Submitted: 29 April 2020

Pinguicula ‘Eye Spy’ is an easy to grow, forgiving hybrid created in 2011 by Stephen Bunclark at Predator Plants, UK. The parentage of *Pinguicula* ‘Eye Spy’ is possibly complex, with certainties of *P. vallesneriifolia* and a giant clone of *P. grandiflora*. When seed from the parent *P. grandiflora* was germinated, one seedling stood out from the batch with larger features in leaf and a corrugated appearance. This now mature seedling was monitored for several years and displays a most interesting flower with electric violet petals and a white inset marked with venation which resembles eye lashes — hence the name ‘Eye Spy’ (Fig. 1).

Pinguicula ‘Eye Spy’ is a cool temperature plant producing multi stages of growth with elongated leaves up to 15 cm long, a starry semi erect shape develops and later in its growth season produces red/purple venation on the leaves, often reducing its surface area to sunlight. More shaded plants will become greener, larger, and less crimped.

Seed is viable, but to maintain the unique character of this cultivar, reproduction should be vegetative only. Since *Pinguicula* ‘Eye Spy’ produces a plentiful supply of gemmae, vegetative reproduction is easy.

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Figure 1: *Pinguicula* ‘Eye Spy’.

Sarracenia purpurea f. *luteola* ‘Super-duper’

Submitted: 9 April 2020

In 2006, Barry Rice germinated some seed of *Sarracenia purpurea* f. *luteola* Hanrahan & Miller, an anthocyanin-free form of *Sarracenia purpurea* subsp. *venosa* var. *burkii* (syn. *S. rosea*), that he received from Bob Hanrahan. A full description of the discovery and characteristics of *Sarracenia purpurea* f. *luteola* was reported in Hanrahan and Miller (1998).

Barry sent several of these seedlings to me. One of these seedlings grew into a large superlative specimen that I have named *Sarracenia purpurea* f. *luteola* ‘Super-duper’. I have grown *Sarracenia* for over 50 years and *Sarracenia purpurea* ‘Super-duper’ is at least twice the size of any *S. purpurea* f. *luteola* that I have seen. The usual comment from expert *Sarracenia* growers is “Wow!”.

Pitchers are light green, total length from crown to lid is 25 cm, lid 10 cm wide and 5 cm tall, pitcher opening 4 cm wide. Flowers are 30 cm tall with petal color initially very light green quickly turning white (Fig. 2).

The word super-duper, defined as of greatest excellence, size, or impressiveness, is a word formation called a rhyming compound, that is, a new word is formed by adding a rhyming word to another word. According to the Merriam-Webster dictionary, the first known use of super-duper was in 1938. Propagation must be by vegetative means to maintain the unique properties of this cultivar.

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Figure 2: *Sarracenia purpurea* f. *luteola* ‘Super-duper’ plant and flower.

Submitted: 9 June 2020

In 2010, I had flowering plants of *Heliamphora neblinae* and *H. folliculata* (Murosipan Tepui) and decided to try and cross the two. Using pollen from the *H. folliculata*, I pollinated the *H. neblinae* flower and soon saw a fruit swelling within. This resulted in several seeds, from which a handful of plants were raised. Eventually, I selected just the two best clones and gave the others away. Of these two, one is far superior to the other, and it is this plant that I think deserves wider recognition and official cultivar status.

Until now known as “*H. neblinae* × *folliculata* Clone 2”, *Heliamphora* ‘Cyclops’ is a large, robust, colorful, and wonderful thing (Front Cover). The pitchers are notably wide and chunky, over 30 cm tall and 10 cm across the open mouth (Fig. 3). Not as upright as its *H. neblinae* mother, but not as decumbent as *H. folliculata*. At up to 3 cm across, the nectar spoon is truly massive (possibly the largest in the genus yet seen?) red in color, downward-leaning into the pitcher and virtually spherical in shape, culminating in a blunt hook at its tip, underneath. The plant seems to concentrate on sheer size, and infrequently forms offsets. A mature, single-crowned plant might produce just one new basal rosette each year. The original plant is now 10 years old and has formed a 10 cm tall, 2 cm thick trunk (a trait I assume originates from the *H. neblinae* parent) and this continues to grow, increasing in height at a rate of about 4 cm a year.

The plant has flowered twice, with several large (7 cm across the tepals) typical, white flowers of the genus held on a stalk around 70 cm tall. Recently, I have been successful in crossing this with *H. exappendiculata*, so its pollen is viable.

The name Cyclops (Greek: “Round Eye”) refers to the huge nectar-spoon which is such a distinguishing feature of this plant. Viewed from the front, the forward-leaning nectar-spoon appears as a solid sphere, without any of its hollow interior visible, looking like a big, red eyeball. In ancient Greek legend and literature, Cyclops was any of several one-eyed giants to whom were ascribed a variety of histories and deeds.

A steady and easy-growing plant under conventional *Heliamphora* conditions, performing well in the greenhouse as well as under both fluorescent and stronger LED lights. Due to its overall height, a mature plant would probably be unsuitable for all but the tallest of terrariums. It flowers less often and produces fewer, but larger pitchers than most other members of the genus. Copious amounts of nectar is produced inside the spoon on warm days and can be seen dripping onto the back wall of the pitchers. Adult plants will require a large pot, at least 20 cm deep and possibly a supporting stake as it forms a trunk; those big, water-filled pitchers are heavy!

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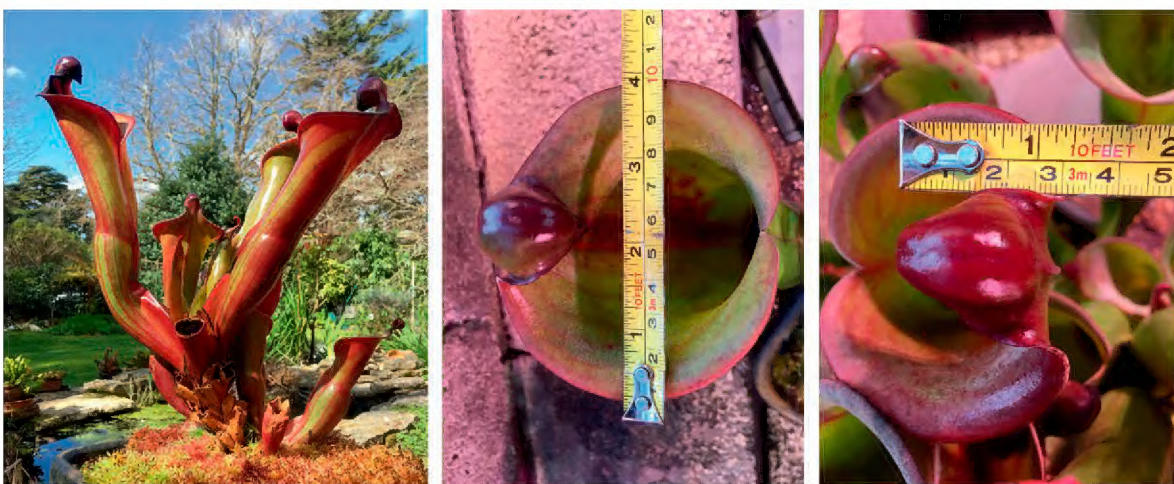


Figure 3: *Heliamphora* ‘Cyclops’.

Dionaea ‘Stove Fire’ (捕蝇草‘炉火’)

Submitted: 7 April 2020

The traps of *Dionaea* ‘Stove Fire’ are incomplete and do not open fully. There are red spots inside and outside the trap. The teeth are long or short and their color is dark red (Fig. 4).

Dionaea ‘Stove Fire’ was named on 18 February 2020 because its teeth are as bright as the fire.

Dionaea ‘Stove Fire’ must be propagated by vegetative division to maintain its unique characteristics.

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Figure 4: *Dionaea* ‘Stove Fire’.

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Sarracenia leucophylla, illustrated by Minelli Lucy France (theorchidartist@outlook.com), a botanical artist and scientific illustrator that specializes in orchids, but has years of experience painting and illustrating a plethora of other flowers and botanicals as well. She works out of her home art studio in Florida, USA.

